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THE ASIAN MICTINI: TAXONOMY, SYSTEMATICS AND BEHAVIOUR IN A TRIBE OF TROPICAL LEAF-FOOTED BUGS (HETEROPTERA: COREIDAE)

by

Nikolai J. Tatarnic ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the

requirements for the degree of Master of Science.

in

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Abstract

The Mictini *sensu stricto* is a tribe of large leaf-footed bugs (Heteroptera: Coreidae) from the Old-World tropics, characterized by elaborate sexual dimorphism. Specifically, males possess enlarged and armed hindlimbs used for male-male combat, and in many species are also endowed with bizarre ventral abdominal tubercles, the function of which is unknown. Spanning the fields of taxonomy, systematics, and ethology, this research explores questions of common ancestry, historical biogeography, and how sexual selection has driven the morphology and behaviour of these insects. Using parsimony analysis, a phylogeny of 27 Asian and 2 African species was reconstructed and the genus *Mictis* was revised. Additionally, two new species of the genus *Priolonomiopsis* were described. Then, focusing on the species *Mictis profana*, sexual dimorphism and allometric relationships were explored in the context of the insect's mating system and behaviour.

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Chapter 1

Introduction

The tribe Mictini *sensu stricto*

The term "Mictini" was originally used to describe a tribe of mostly tropical coreids characterized by the possession of incrassate hind femora in males but not in females (e.g. Amyot and Serville 1843, Lethierry and Severin 1894, O'Shea 1975). It has since been shown that this is probably not a monophyletic group (O'Shea and Schaefer 1978), and in his generic revision, O'Shea (1975) differentiated between the Mictini *sensu lato* and *sensu stricto*; the former describing the polyphyletic grouping as above, and the latter describing a proposed monophyletic group of genera restricted to the Old World tropics and the South Pacific. This Old World grouping had previously been suggested by Kirkaldy (c. 1910, unpublished manuscript, see below) and Bergroth (1913). The Mictini *s.s.* was further subdivided into four 'natural groups', two Asian and two African. In Asia, the Mictini are represented by the "Natural Groups" Mictis and Derepteryx; males of the former are characterized by the possession of median and lateral abdominal tubercles, and of the latter by the absence of abdominal tubercles and the possession of extremely extended humeral projections (O'Shea and Schaefer 1980). However, species placed within each group provide several exceptions to these rules (e.g. *Priolonomiopsis amplicollis* of the Derepteryx group has two median abdominal tubercles, *Mictis farinulenta* of the Mictis group has pronounced humeral angles).

The most comprehensive review of literature on the Mictini is that of O'Shea (1975), who included all records listed in the Zoological Record up to and including

1970. He also included several records not found therein, and contributed several important works himself based on his PhD dissertation, in particular his generic revisions of the Asian and African Mictini (1980a,b), which described all the known genera and listed all included species from these regions. O'Shea (1975) and O'Shea and Schaefer (1978) divided previous taxonomic work into four categories:

1. Catalogues and checklists of the Coreidae in general (Amyot and Serville 1843, Lethierry and Severin 1894, Bergroth 1913, and Kirkaldy c. 1910: this last reference is an unpublished manuscript of uncertain date, a copy of which is in the care of J.A. Slater at the University of Connecticut).
2. Works on the higher classification of the Coreidae (Stål 1870, 1873, Schaefer 1965, and Kumar 1965).
3. Faunal descriptions of restricted areas (Distant 1890-93, Central America; Alayo 1967, Cuba; VanDuzee 1917, Blatchley 1926 and Torre Bueno 1941, North America; Schouteden 1938, Villiers 1952, Central Africa; Dispons 1962, 1963, 1964, and Hsiao 1963a,b, 1964, 1965, Southeast Asia and China).
4. New species and generic descriptions.

Other useful references include various published lists of museum collections, some of which provide excellent diagnoses, new species description and illustrations (e.g. Dallas' list of specimens in the British Museum (1852), Blöte's 1938 list of specimens in the Rijksmuseum, Netherlands).

Recent publications on the Mictini are few and far between. The only new taxonomic contributions I have been able to find are a few new species descriptions by

Brailovski (2002a) and Brailovski and Barrera (2000, 2001) well as that of a new genus of Mictini from Australia (Brailovski 2002b). To date there have been only two known phylogenetic analyses of the Mictini; the first is included in the PhD thesis of O'Shea (1975), and the other, by Li is based solely on Chinese taxa (1994).

Biology of the Mictini

Very little is known about the behaviour and life history of these insects, although a few species are known pests and as such have caught the attention of researchers. Schaefer and Mitchell (1983) and Schaefer and O'Shea (1979) determined the host plants of many species of Mictini, and some work has been done on the composition of metathoracic scent gland secretions(e.g. Waterhouse *et al.* 1961, Waterhouse and Gilby 1964,) as well as on ventral abdominal gland secretions (Aldrich, unpublished). The most prolific body of research has been into the biology of the Crusader bug, *Mictis profana*, as it is considered to be both a pest of crops throughout its range and a potential biological control agent of *Mimosa pigra* in Australia (Flanagan 1994). This body of work also includes the study of "osmotic pump" feeding by this species, (Miles and Taylor 1994), the composition and variability of its saliva (Taylor and Miles 1994), metathoracic scent gland composition of this and other species (Waterhouse *et al.* 1961, Waterhouse and Gilby 1964), and the determination of parasitoids of Australian coreids, including *M. profana* and *M. caja* (Naumann and Steinbauer 2001). However, a listing of the worldwide fauna and knowledge of mating and fighting behaviour, defensive mechanisms, evolutionary pressures and evolutionary history is far from complete.

Secondary sexual characters

Mictines are characterized by elaborate sexual dimorphism, with males displaying incrassate hind femora, spined hind tibiae and in many species, elaborate ventral abdominal tubercles. In other coreids, hindlimb modifications in males function in male-male combat (e.g., Mitchell 1980, Miyatake 1997, Eberhard 1998), and exhibit highly allometric scaling relationships with respect to body size (Miyatake 1997, Eberhard 1998). In addition to the tribe Mictini, males of the Acanthocorini and Petascelidini also possess prominent ventral abdominal tubercles (O'Shea and Schaefer 1978), though neither the function of these tubercles nor their origin is known. Studies of the scaling relationships of dimorphic structures coupled with behavioural observations and experiments may help to elucidate what selective pressures have led to the elaborate variety of structures expressed throughout the Mictini.

Scent glands

Coreid nymphs and adults produce potent defensive chemical secretions and as a result are not expected to suffer significant predation or parasitism (Steinbauer 1999, Steinbauer & Davies 1995) (but see Chapter 5 for an account of predation of *M. profana* nymphs). When captured, both adults and juveniles immediately release a strong, sweet odour from their metathoracic scent glands. The defensive compounds produced are a mix of hexan-l-yl acetate, hexanal, haxan-l-ol and acetic acid (Waterhouse and Gilby 1964), and in one species of coreid have been shown to kill a tarantula when placed in a confined enclosure (Torre Bueno and Ambrose 1936).

Male coreids also possess a ventral abdominal gland (VAG), which opens on the 7-8th intersegmental membrane (Aldrich *et al.* 1982), and appears to secrete species-specific blends of aromatic alcohols (Aldrich *et al.* 1976). The function of these secretions is uncertain, but they may function as aggregation pheromones or as mate attractants. The possible functions of VAG secretions in *M. profana* are discussed further in Chapter 4.

The biology of *Mictis profana*

Because much of this thesis deals with work on *M. profana*, it is appropriate to provide background information about this species in some detail. Found only in the Old World, members of the tribe Mictini feed mostly on the fruits and young shoots of legumes (Schaefer and O'Shea 1979, Schaefer and Mitchell 1983). While most members of the tribe are restricted to Southeast Asia, *Mictis profana* is also found in Australia and throughout the South Pacific. In many parts of its range it is considered a pest of significant economic importance. Some efforts have been made to determine whether the Crusader bug may be a candidate for biological control; in Australia *M. profana* is known to be parasitized by several Hymenopterans: *Chrysochalcissa olivacea* Girault (Torymidae), *Anastus* sp. nr *pentatomidivorus* Girault (Eupelmidae), *Ooencyrtus caurus* Huang & Noyes (Encyrtidae) and *Gryon pentatomum* (Dodd) (Scelionidae) (Naumann and Steinbauer (2001). At the same time, *M. profana* is also being considered as a biological control agent for *Mimosa pigra* in Australia (Flanagan 1994).

Mimicry and deflective patterning

Nymphs of *Mictis profana* are brightly coloured with orange and black patterning, presumably an aposematic warning of their unpalatability to would-be predators. As a further barrier to being ingested, many coreids, including the mictines, have foliacious tibial, antennal and pronotal projections, which may help to break up their silhouette and impede detection. Alternatively, these flattened expansions might actually be examples of deflective patterning, whereby potential predators are made to focus on appendages rather than on the body of prey species (Schuh and Slater 1995:31). Tibial dilations in adults occur predominantly on the hindlimbs and are often sexually dimorphic, whereas nymphs of many species may also have markedly dilated fore- and mid-tibiae, which usually become greatly reduced with age. Kumar (1966) hypothesized that these dilations assist nymphs in escaping from predators by helping them float gently to the ground, however because the nymphs are so small and light it is unlikely that such modifications would be necessary to slow their descent.

In many species the apical antennal segments are brightly coloured. When threatened, disturbed nymphs and adults of *Mictis profana* will vibrate their antennae vigorously (Chapter 4). This may further assist in diverting a potential predator's attention away from the insect itself, or may even be an example of wasp mimicry, which is quite common in the Heteroptera (Schuh and Slater, 1996).

While the young of some species are brightly coloured as noted above, O'Shea (1975: 29) stated that "most [adult] Mictini are brown…whereas none is aposematic." In

Chapter 2 I show that this is not the case, and describe bright aposematic colouring in all species examined.

Thesis Objectives

Spanning the fields of taxonomy, systematics, and ethology, this thesis explores questions of common ancestry, historical biogeography, and how sexual selection has driven the evolution of morphology and behaviour of these insects. Through parsimony analysis using morphological data. In Chapter 2, I test our current understanding of species group relationships between Asian and African taxa, revise the Asian genus *Mictis* and describe two new species of Mictini from Southeast Asia. Then in Chapter 3 I examine scaling relationships and sexual dimorphism of various body structures using the species *M. profana*. Chapter 4 extends the study of sexual selection in this species, through detailed behavioural studies of mating and male-male combat. Lastly, in Chapter 5 I consider the status *M. profana* as a crop pest in Fiji, and discuss field observations relating to its possible biological control.

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Chapter 2

Phylogeny of the Asian Mictini

Introduction

The Mictini *s.s.* is a tribe of large coreid bugs (Heteroptera: Coreidae) from the Old-World tropics, characterized by the possession of incrassate hind femora in males but not in females. In addition, many males also possess lateral and median ventral abdominal tubercles. O’Shea (1975) described four natural groups of genera within the Mictini *s.s.* which he presumed to be monophyletic. He reconstructed the phylogenetic relationships among these four natural groups apparently using only seven characters (Fig. 2.1). He proposed that the Plectropoda Group from Africa was the sister to the Asian Mictis Group, and that these two together formed the sister to the Derepteryx Group of Asia and the Anoplocnemis Group of Africa combined. O’Shea also reconstructed the phylogenies of each of the natural groups using a method described by Ashlock (1972), based on Camin and Sokal (1965). These four analyses were each based on the same 26 morphological characters which were “subjectively weighted as being most important” (O’Shea 1975:126), with only one tree of “several” reported for each group.

The field of phylogenetic systematics has changed much since then, and more advanced formal methods are now used to explore relationships among taxa. When re-analysed under parsimony in PAUP* 4.10b (Swofford 2002), O’Shea’s dataset yields over 60,000 equally parsimonious trees (heuristic searching, tbr branch swapping, random addition, 100 replicates). A consensus of these trees is for the most part uninformative and has almost no branch support, but the results do not support the current natural groups.

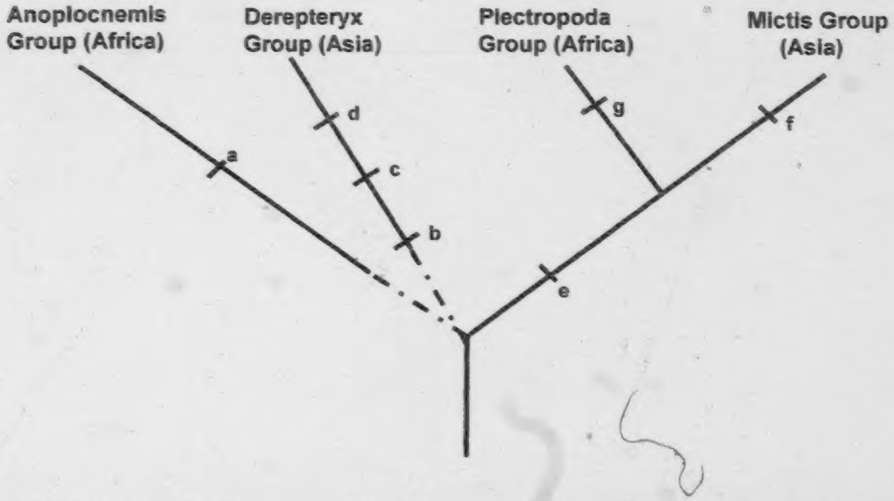


Figure 2.1. Phylogeny of the proposed natural groups of genera within the Mictini s.s. Seven characters are used: a) stout antennae, b) dilated tibiae, c) enlarged humeral lobes, d) tuberculate femora, e) lateral tubercles on abdominal segment III of male, f) median abdominal tubercle, and g) lateral tubercles on abdominal segments III and IV of male. No apomorphic characters were found to link the Anoplocnemis and Derepteryx Groups, reflected here by the broken lines and the trifurcation at the basal node (from O'Shea 1975).

In the work presented here I explore 1) relationships within the genus *Mictis* Leach, 2) relationships among members of the Mictis Group, including two undescribed species from Southeast Asia 3) the relationship of the Mictis Group to both the Derepteryx and the Plectropoda Groups, and 4) how these phylogenetic constructions relate to the geographic distributions of the included species. If the current taxonomic arrangements based on O'Shea's hypotheses are correct, the resulting most parsimonious reconstruction should demonstrate the monophyly of the genus *Mictis* within the larger

Mictis Group, which together should be most closely allied to members of the Plectropoda Group. In addition, the Mictis+Plectropoda group should be rooted at the Asian Derepteryx Group. Comparison of the distribution data for the included species to the proposed phylogenies will help both in assessing the likelihood of the phylogenetic reconstructions and in establishing a possible scenario for the biogeographic origins of the Mictini in Asia.

Materials and Methods

Taxa

O'Shea and Schaefer's (1980) revision of the genus *Mictis* included 19 species, 12 of which are included in this analysis. Based on original species descriptions, catalogues as well as comments by O'Shea and Schaefer, all but one of the species excluded from this study can be allied to included species as either sister taxa or even as synonyms thereof. Briefly: *Mictis angusta* Hsiao (1965) is said to be allied to *M. tenebrosa* (Hsiao 1965); *M. dilatipes* Blöte is described by O'Shea and Schaefer (1980) as differing only in colouration from *M. profana* (Fabr.); *M. macra* Stål is said by Distant (1902) to be almost identical to *M. gallina* Dallas but with less incrassate hindlimbs; the description of *M. tridentifer* Blöte (1938) accurately describes *Neomictis filicornis* (O'Shea); Hsiao's description and illustrations of *M. tuberosa* (1965) suggest that this species is almost certainly synonymous with *M. longicornis* Westwood; *M. serina fuscipes* Hsiao is presumably the sister species to *M. serina* Dallas. It is only *M. falloui* Reuter that is problematic because its description is insufficient to infer a likely relationship to any particular species included in my analyses. More recently, Brailovski (2002) described two new species of *Mictis* from Sulawesi, however based on his descriptions and illustrations, these appear more akin to the genus *Xyrophoreus* and are not included in this study. As well, two previously undescribed species of Mictini from Sumatra and Sarawak are included in the analysis.

In addition to *Mictis*, several other genera from the Mictis, Derepteryx and Plectropoda Groups are included. Members of the Mictis Group used in this analysis outside the genus *Mictis* are: *Aspilosterna acutangula* (Stål), *Mercennus gracilis* (Westwood), *Neomictis filicornis* (mentioned above), *Notobitopsis aruana* (Distant), *N. militaris* (Distant), *Pseudomictis distinctus* Hsiao, *P. oblongipes* Xiang, *Pternistria sexlineata* Horvath and *Xyrophoreus tonsor* Breddin. The African Plectropoda Group is represented by *Plectropoda bicolor* Haglund and an unidentified species of *Elasmopda* Stål. The presumably more distant Derepteryx Group from Asia is represented by four species: *Molipteryx hardwickii* (White), *Ochrochira pallescens* (Distant), *Priolonomia gigas* Distant, and *Priolonomiopsis amplicollis* (Stål).

Pinned and dried specimens were obtained on loan from several institutions, including: the ROM, Toronto; Ontario, the American Museum of Natural History, New York; the Bishop Museum of Natural History, Hawaii; the National Museum of Natural History, Smithsonian Institution, Washington, D.C.; the Universiteit van Amsterdam, Zoölogisch Museum Amsterdam, Netherlands; the California Academy of Sciences; and the Natural History Museum, London. Additionally, three species (*Mictis longicornis, M. tenebrosa and M. profana*) were collected by myself in Gunung Halimun National Park, West Java, Indonesia (1998) Bach Ma National Park, Vietnam (2001) and Vanua Levu, Fiji (2001-2002), respectively.

Characters

In total, 64 structural characters were coded for this analysis. These comprise mostly external characters of males as well as characters of the aedeagus and paramere, and where available, characters of female hindlimb structure. Characters were chosen based in part on earlier work by O'Shea (1975), O'Shea and Schaefer (1978, 1980) and Li (1994). Although it would have been preferable to include molecular data as well, the age and condition of many of the specimens and the temporal constraints of this study precluded such efforts.

In cases where multiple specimens were available, potential characters found to vary within any given species were excluded from further analysis. For species represented by single specimens it was necessary to assume that these represented the typical condition of the species as a whole.

Unknown states were coded as missing using "?", while inapplicable states were coded as "0" (as suggested by Maddison 1993). Inapplicable character states can be problematic, as they are treated by phylogenetics programs in the same manner as missing data unless they are coded as a distinct state unto themselves. In this dataset care was taken to avoid such difficulties and only four characters with inapplicable states were included herein. One means of avoiding inapplicable character states was to code several characters as multistate. Because of uncertainty in assessing relationships among states, all multistate characters were treated as unordered for all analyses (Appendix 1).

Male genitalia

Kumar (1965), Schaefer (1965), O'Shea (1975) and O'Shea and Schaefer (1978) all described difficulty in inflating the male genitalia in the mictines, since the sclerotized processes frequently tear the conjunctiva during manipulation, preventing further inflation. The following is a brief description of the methods I have found most successful for aedeagal inflation.

Male genitalia were removed and dissected using modifications of the methodologies described by O'Shea and Schaefer (1978) and Packauskas (1994). Pinned insects were floated on a small Styrofoam raft in a beaker of freshly boiled water, angled such that only their terminal abdominal segments were submerged underwater. Insects were left like this for only a few minutes (time was not crucial), then removed from the beaker. At the same time, a small screw-top vial 1/3 full of 10% KOH was warmed in the beaker of water. Using forceps, the end of the abdomen was gently squeezed dorsoventrally, thereby exposing the genital capsule. The intersegmental membrane between the 8th abdominal segment and the genital capsule was severed with a scalpel and the genital capsule removed. The entire genital capsule was transferred to the vial of KOH, which was then returned to the hot water beaker. After about one minute, the genital capsule was removed from the KOH and placed in a Petri dish of distilled water. Under a dissecting scope, one pair of curved jeweller's forceps was used to hold the genital capsule still, while with another pair of forceps the capsule was dorsoventrally squeezed and released repeatedly. This generally caused muscle tissue to be ejected from the capsule in large clumps, which were then cleared away. After this cleaning, the parameres were removed from the capsule by gently tearing them away with fine forceps. To remove the aedeagus, one pair of straight forceps held the mouth of the genital capsule, while a second pair of curved forceps were inserted blindly into the cranial opening of the capsule. By gently scraping the curved outer edge of the forceps tips along the ventral inner surface of the capsule, ligaments holding the phallobase in place were severed. Once these were broken, the aedeagus could be grasped with the forceps and pulled away from the capsule. By gently squeezing the aedeagus dorsoventrally as close to the base as possible, one could eventually coax the aedeagal sacs to evert and inflate, thereby exposing them, their associated sclerites and the vesica.

Any puncturing or tearing of the aedeagus generally led to failure to inflate. The genitalia of several species proved impossible to inflate, and genitalic characters had to be exposed by destructively dissecting the uninflated aedeagus. Aedeagi which were successfully inflated were photographed frontally and laterally for reference. Parameres, which were much easier to remove, were illustrated for character scoring. In a few instances images and descriptions from O'Shea (1975) and O'Shea and Schaefer (1980) were used to code genitalic characters when dissections were not available.

Cladistic analysis

The phylogenetic analyses were performed in PAUP* 4.10b (Swofford 2002), using maximum parsimony, with the general heuristic search procedure (random addition sequence, tbr branch swapping, 100 repetitions). Tree robustness was assessed in PAUP* via bootstrap and jackknife procedures (default settings, 100 repetitions), while Bremer Decay Indices were calculated in PAUP using TreeRot version 2 (Sorenson 1999) to generate the input files.

To test O'Shea's phylogenetic relationships among species groups, trees were first rooted at the Derepteryx Group, then at the Plectropoda Group. Phylogenetic reconstructions were also used to assess the monophyly of the genus *Mictis* and the various species groups, and to aid in the taxonomic placement of the two new species included in the data.

Geographic distributions

Distribution data was collected from O'Shea's thesis (1975) and subsequent publications (1980a,b, O'Shea and Schaefer 1980), from numerous catalogues and species descriptions (Blöte 1938, Breddin 1909, Dallas 1852, Dispons 1963, 1964, Distant 1902, Horvath 1911, Hsiao 1963a,b, Stål 1965 and Xiong 1987), from museum specimen labels as well as from personal collection data (Table 2.1). Some of the species distributions will almost certainly be incomplete, but, if nothing more, this comprehensive compilation provides a basis for subsequent work. Biogeographic regions were identified based on Turner *et al.*'s (2001) work on the biogeography of Southeast Asia (Figure 2.2).

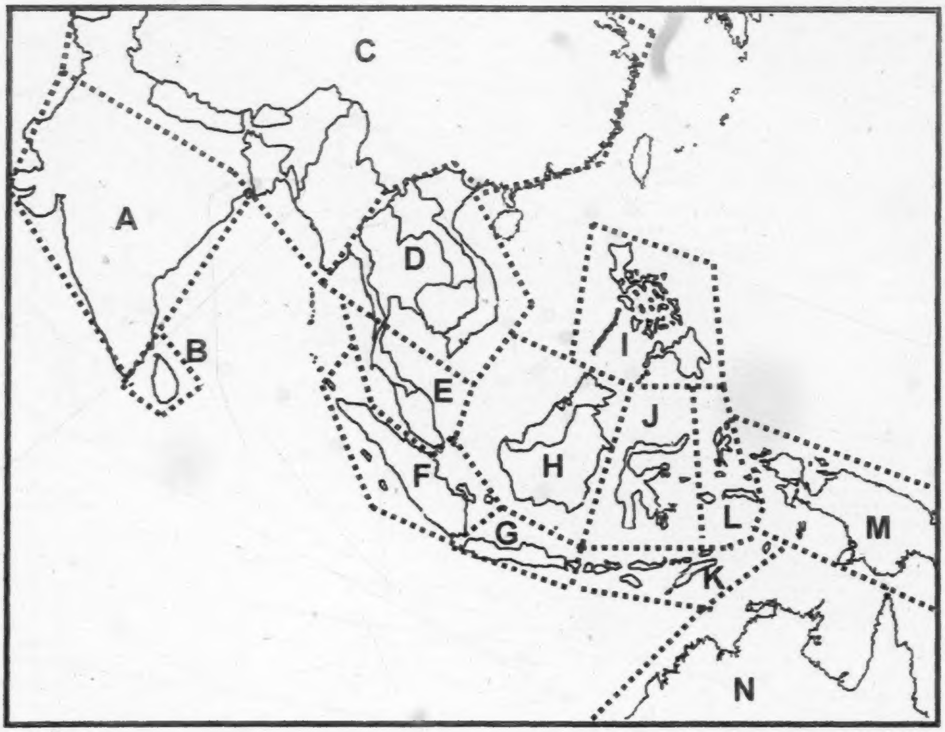


Figure 2.2. Areas of endemism, based on Turner *et al.* (2001). A) India, B) Sri Lanka, C) Himalayas, Burma, Southern China, D) Southeast Asia, E) Malay Peninsula, F)Sumatra, G) Java, H)Borneo, I) Philippines, J) Sulawesi, K) Lesser Sunda Islands, L) Molucca, M) New Guinea, N) Australia. Areas not shown on map: O) South Pacific, P) Africa.

Table 2.1. Distribution data for study species, including species of *Mictis* not included in this study. Areas of endemism are based on Turner *et al.* (2001). A) India, B) Sri Lanka, C) Himalayas, Burma, Southern China, D) Southeast Asia, E) Malay Peninsula, F)Sumatra, G) Java, H) Borneo, I) Philippines, J) Sulawesi, K) Lesser Sunda Islands, L) Moluccas, M) New Guinea, N) Australia, O) South Pacific, P) Africa. (**) Indicates taxa not included in this study, while (†) denotes the two previously undescribed species from Sarawak and Sumatra.

		Areas of Endemism															
	Species	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P
1	*Mictis amboinenses* Walker												*				
2	*Mictis angusta* Hsiao**			*													
3	*Mictis caja* Stål														*		
4	*Mictis dilatipes* (Blöte)**											*					
5	*Mictis discolor* Dallas									*							
6	*Mictis falloui* Reuter**			*													
7	*Mictis farinulenta* Breddin									*		*					
8	*Mictis formidabilis* Distant		*														
9	*Mictis gallina* Dallas	*		*	*												
10	*Mictis longicornis* Westwood					*		*	*	*							
11	*Mictis macra* Stål**	*															
12	*Mictis oceanensis* Distant															*	
13	*Mictis profana* (Fabricius)							*			*			*	*	*	
14	*Mictis pungens* Stål									*							
15	*Mictis serina* Dallas			*													
16	*Mictis tenebrosa* (Fabricius)	*		*	*												
17	*Mictis tridentifer* Blöte**						*										
18	*Mictis tuberosa* Hsiao**			*													
19	*Aspilosterna acutangula* (Stål)				*	*											
20	*Mercennus gracilis* Westwood					*		*	*								
21	*Neomictis filicornis* Walker						*		*								
22	*Notobitopsis aruana* (Distant)													*			
23	*Notobitopsis militaris* (Distant)													*			
24	*Pseudomictis distinctus* Hsiao			*	*												
25	*Pseudomictis obtusispinus* Xiong			*	*												
26	*Pternistria sexlineata* Horvath													*			
27	*Xyrophoreus tonsor* Breddin	*	*														
28	*Molipteryx hardwickii* (White)	*		*	*												
29	*Ochrochira pallescens* (Distant)	*		*	*												
30	*Priolonomia gigas* Distant	*		*	*												
31	*Priolonomiopsis amplicollis* (Stål)	*															
32	*Priolonomiopsis sarawensis* n.sp. †								*								
33	*Priolonomiopsis sumatra* n.sp. †						*										
34	*Plectropoda bicolor* Haglund																*
35	*Elasmopoda sp.* Stål																*

Characters, Coding and Phylogenetic Significance

I identified and used 64 characters for the phylogenetic reconstructions presented here. In the character analysis provided below I describe each character, explain their codings and summarize their significance in the reconstructions presented in the next section.

Male genitalia and genital capsule:

Male genitalic characters have proven useful in grouping many insect taxa. Schaefer (1965) states that within the Coreidae, shape and structure of the paramere and aedeagus are extremely useful in higher level taxonomy, and in some cases may be useful at the generic and species levels as well.

Paramere (1 – 5) – Within the Coreidae, parameres vary greatly in form and may be unsclerotized as in the Acanthocerini, or moderately to strongly sclerotized, as in the Mictini and the Nematopodini (O'Shea and Schaefer 1978). In *Mictis* and related genera, parameres are strongly sclerotized and highly variable in shape, ranging from relatively short, angular and stout to long, thin and scythe-like. Because of this high variability, paramere characteristics are mostly useful in determining some terminal relationships, but are less useful across wider ranges of taxa (Fig. 2.3).

There is no clear terminology for various regions of the coreid paramere. In this analysis I use 'paramere body' to describe the large, more or less rectangular base of the paramere, while 'arm' is used to describe the thinner terminal branch of the paramere.

Paramere orientation is considered in terms of how the paramere rests within the genital capsule: 'inner margin' refers to the edge of the paramere toward which the arm is curved and 'outer margin' describes the opposite side. 'Inner concavity' refers to the concave region on the upper surface at the base of the arm. Five characters of male parameres were coded as follows:

1. *Paramere*: **(0)** dorsal concavity without prominent rectangular tubercle ; **(1)** dorsal concavity with a prominent rectangular tubercle.

A prominent rectangular tubercle within the inner concavity of paramere is shared by *Mictis longicornis, M. gallina* and *Neomictis filicornis*. It is not seen in *M. pungens*, though in other respects the paramere is quite similar. I have not seen the paramere of *M. formidabilis*, but I predict it might share this feature.

2. *Paramere: inner surface*: **(0)** unmodified; **(1)** heavily wrinkled.

A distinctive wrinkling within the concavity of the paramere unites *Mictis longicornis, M. pungens, M. gallina* and *Neomictis filicornis* (*M. formidabilis* is unknown). This is also expressed in *Mictis tenebrosa*, the unknown species from Sumatra and *Priolonomiopsis amplicolis*, as well as the two genera *Pseudomictis* and *Notobitopsis*.

3. *Paramere: tip*: **(0)** thin and tapered; **(1)** broad and compressed.

Compression of the paramere tip is seen in *Mercennus gracilis* and both species of *Notobitopsis*, as well as *Elasmopoda* sp. In the latter, this condition is taken to the extreme, with the entire paramere shovel-shaped.

4. *Paramere: arm*: **(0)** broad and flat ; **(1)** curved, thickened at base, then evenly tapering to a thin point ; **(2)** angular, short and tapered ; **(3)** angular, tip broad and flattened, thumb-like bump at base.

Within the Mictini, the paramere arm is generally evenly curved inwards and upwards, thickened at the base and tapering to the tip. In *Mictis profana* and *M. amboinensis* the paramere tip is relatively short, angular and tapered, while in both species of *Notobitopsis*, and to some extent in *Mercennus gracilis*, the arm is broad, flattened and angular with a thumb-like knob at the base.

5. *Paramere: body*: **(0)** outer margin straight; **(1)** outer margin strongly humped.

In several taxa the outer margin of the paramere is strongly arched, giving the paramere a claw-like appearance. This character unites several species of *Mictis* with the Derepteryx Group and *Aspilosterna acutangula*.

Aedeagus (6 – 11) – Characters of the coreid aedeagus include a helical sclerotized vesica within a conjunctiva, which is divided into several membranous eversible sacs. When inflated, these sacs can vary in shape, size, and relative position, and may possess unsclerotized to strongly sclerotized ventral, lateral or dorsal processes. The Mictine aedeagus typically possesses a bifurcate distodorsal sac (the tip of which is frequently forked), large, paired distoventral sacs and often large distolateral sacs. The distolateral sacs are occasionally pronounced and project outwards, and often have weakly to strongly sclerotized lateral processes, which range from light sclerotization of the edge of the lateral lobe, to distinct knobs or plates. Sclerotization may also be seen on the tips of the dorsal sac, as in *M. discolor* (Fig. 2.5c), and on the ventral sacs, as in the genus *Molipteryx* (Fig. 2.8b).

While coreid aedeagi may be fairly elaborate in structure, it is not certain what the function of these genitalic modifications might be, although the high levels of genitalic variability suggest that the genitalia may be under significant levels of sexual selection, perhaps via cryptic female choice (Eberhard 1993, 1994) or sexual conflict (Clutton-Brock and Parker 1995). Within the Mictini, characters of the aedeagus are quite variable and only provide some evidence in resolving sister relationships. Successfully inflated aedeagi are shown in figs. 2.4 through 2.8. Six characters of the aedeagus were coded as follows:

6. *Aedeagus: lateral processes*: **(0)** absent or unsclerotized; **(1)** lateral processes sclerotized.

Lateral sclerotized processes are virtually ubiquitous, with only the Derepteryx Group, *Priolonomiopsis amplicollis*, *Pternistria sexlineata, Neomictis filicornis* and the unidentified species from Sarawak lacking them (though not examined, it is suspected that *M. oceanensis* and *M. formidabilis* both have sclerotized processes). These processes are quite variable in shape, yet this variation is of little use in resolving relationships.

7. *Aedeagus: lateral sacs*: **(0)** not pronounced; **(1)** distinct, projecting outward.

In several species, the distolateral lobes are extended upwards and outwards. This trait unites *M. longicornis, M. pungens* and *M. gallina* with *M. discolor, Aspilosterna* *acutangula* and *Priolonomia gigas*. *Xyrophoreus tonsor*, *Pternistria sexlineata* and *M. farinlenta* also exhibit this trait.

8. *Aedeagus: dorsal sac*: **(0)** broad at the base then sharply tapered; **(1)** very long and thin.

A long, narrow distodorsal sac is autapomorphic for the genus *Notobitopsis*.

9. *Aedeagus: dorsal sac*: **(0)** not forked; **(1)** tip forked.

In almost all taxa the distodorsal sac of the aedeagus is at least somewhat forked. The lack of a forked distodorsal sac is shared by *Priolonomiopsis amplicollis* and the new species from Sumatra and Sarawak, as well as *Molipteryx and Ochrochira pallescens.*

10. *Aedeagus: dorsal sac*: **(0)** without thin lateral projections; **(1)** with thin lateral projections.

Based on this analysis, lateral projections emanating from the distodorsal sac appear to be convergent in *Ochrochira pallescens* and *Pternistria sexlineata*.

11. *Aedeagus: ventral sacs*: **(0)** small or absent; **(1)** prominent; **(2)** sclerotized.

Almost all taxa sampled possess divided distoventral sacs. Distoventral sacs are either quite small or absent in only a few taxa, notably; the genera *Pseudomictis and Notobitopsis*, *Priolonomiopsis amplicollis* and *Neomictis filicornis*. O'Shea and Schaefer (1980) state that within the genus *Mictis* distoventral sacs are absent. Despite this claim, these sacs are present and rather well-developed in all species of *Mictis* sampled.

Genital capsule (12 – 14) – The 9th abdominal segment is most variable along its posterior rim, which may form a distinct upturned or downturned lip, may be grooved, deeply cleft, or possess paired projections against which the parameres rest. Additionally, in some species the genital capsule is projected caudally, sometimes forming a distinct shelf. This structure can be useful in species identification, but its notable variability limits the phylogenetic usefulness of this character.

Three characters of the male genital capsule were coded as follows:

12. *Genital capsule*: **(0)** not produced posteriorly; **(1)** produced posteriorly.

In some cases the ventral margin of the genital capsule is projected caudally, however this trait appears to have arisen several times and does not provide much useful phylogenetic information. This is most noticeable in the both species of *Notobitopsis*, *Pternistria sexlineata, Elasmopoda* sp., the new species from Sumatra, *Neomictis filicornis, Molipteryx hardwickii* and *Priolonomia gigas*.

13. *Genital capsule*: **(0)** smooth; **(1)** grooved or cleft.

Throughout the taxa sampled, a longitudinal groove or cleft in the genital capsule is prevalent. A lack of this feature helps to unite *Aspilosterna acutangula* with *Molipteryx hardwickii* and *Priolonomia gigas*, though not with *Ochrochira pallescens*.

14. *Genital capsule*: **(0)** without distinct lip; **(1)** with distinct lip; **(2)** with downturned lip.

A little over half of the taxa sampled express a distinct lip along the margin of the genital capsule. This lip is distinctly curved downwards in the clade *Mictis amboinensis*, *M. profana* and *M. caja*, a feature which is also shared by the more distant *M. serina*.

Most other species of *Mictis* lack this lip, as do *Aspilosterna acutangula, Plectropoda bicolor, Priolonomiopsis amplicollis* and the Derepteryx Group.

Characters of the head:

There are several characters of the head that are said to be useful in the higher classification of the Coreioidea, unfortunately many of these are not variable within the Asian Mictini. For example, Schaefer (1965) describes "a protuberance or ridge closely applied to the eye", and O'Shea and Schaefer (1978) state that this postocular tubercle is found in few Mictine genera, yet in all of the genera examined for the present study such a tubercle is ubiquitous. This character was actually used by both O'Shea (1975) and Li (1994) for phylogenetic analyses, however after careful examination of the same taxa it is unclear to me how character states were determined. There are very few characters of the head that vary consistently enough to be used in this phylogenetic analysis, although some antennal characters, proboscis length, relative extension forward of the clypeus and the degree of separation between antennifers are somewhat useful.

Three antennal characters, one character describing the antennifers and two mouthpart characters were coded as follows:

Antennae (15 – 17)

15. *4th antennal segment*: **(0)** short, thick and straight; **(1)** roughly equal in length to segment I, thin and curved; **(2)** much longer than segment I, thin and curved.

The terminal antennal segment shows a good deal of variation throughout the taxa sampled. Extremely short, straight and stout terminal segments help to define the clade of *Mictis profana, M. amboinensis, M. caja, M. oceanensis* and *M. farinulenta*. Short terminal segments also unite the two African taxa, and are also seen in *Xyrophoreus tonsor*. In individuals of almost all the other taxa the terminal segment is curved and at least as long as the first antennal segment. The group of *Mictis longicornis, M. pungens, M. gallina* and *Neomictis filicornis* is supported by the possession of rather long, thin curved terminal segments.

16. *4th antennal segment*: **(0)** not coloured; **(1)** yellow at tip or entirely yellow.

In many taxa the terminal antennal segment is either partly or wholly yellow. This trait is shared by many of the taxa associated with *Mictis profana*, as well as several of the taxa associated with *M. longicornis*. Several other species show this character, and it is unclear whether this has arisen several times or is actually representative of multiple losses.

17. *3rd antennal segment*: **(0)** straight; **(1)** dilated.

In the taxa sampled only *Priolonomia gigas* displays a dilated third antennal segment, though this character is common to many other taxa not included in this study.

18. *Antennifers*: **(0)** touching or very close together; **(1)** widely separated.

For the most part the antennifers are situated wide apart, although within the genus *Mictis*, closely placed antennifers appear to be more common, with the exception of the grouping of *M. longicornis, M. gallina* and *Neomictis filicornis*, as well as *M. caja*.

Mouthparts (19 – 20)

19. *Proboscis*: **(0)** short; **(1)** almost reaches middle coxae.

In most of the taxa studied the proboscis reaches or almost reaches the middle coxae. A short proboscis is infrequently seen, and only provides weak support for a few terminal groupings.

20. *Mandibular plate*: **(0)** surpassed by preclypeus; **(1)** level with preclypeus; **(2)** extends beyond preclypeus.

When viewed from the side, the projections forward of the mandibular plate and the preclypeus were used by Li (1994) in his phylogeny of Asian Mictini. Within the present study, the mandibular plate and the preclypeus being level with one another provides some phylogenetic support, and helps to *join Priolonomiopsis amplicollis* and the two new species with *Plectropoda bicolor, Pternistria sexlineata* and *Pseudomictis obtusispinus*. This is also seen in *Mictis profana* and *M. farinulenta*. In only two species, *Pseudomictis distinctus* and *Aspilosterna acutangula*, does the mandibular plate extend beyond the preclypeus, a condition which does not appear to be synapomorphic in these species.

Characters of the thorax:

Pronotum (21 – 29) – Because there is no consistent terminology for the coreid pronotum, the terminology used herein is taken from O'Shea and Schaefer (1978). The pronotal collar, when viewed from above is a lateral furrow immediately behind the cranial margin of the pronotum. In most species the collar is a deep lateral sulcus, while in a few species it is shallow and difficult to see. From the head, the pronotum extends backwards, angling upwards and flaring out to the sides. In most cases, the pronotal angle is greater than 50^0, while in a few taxa the pronotal angle is substantially less steep. At its widest point, the pronotum is usually extended somewhat farther than the width of the body, occasionally into broad wing-like lobes, which may be projected upwards and/or forwards. The humeral angles are rarely rounded, and are usually subacute or sharply pointed. Lateral margins of the pronotum vary between smooth, nodulose, serrated and jaggedly serrated. Pronota are illustrated in figure 2.10. Pronotal characters for the new species from Sumatra (= *Priolonomiopsis sumatra*) and Sarawak (= *P. sarawensis*) can be seen in the habitus drawings in figures 2.18 and 2.19 respectively. Nine pronotal characters were coded as follows:

21. *Collar*: **(0)** indistinct; **(1)** distinct.

When viewed from above, the pronotal collar is a sagittal furrow immediately caudal to the anterior margin of the pronotum. A distinct pronotal collar helps to join most species of *Mictis*. Outside of *Mictis*, both species of *Notobitopsis*, *Pternistria sexlineata* and the Derepteryx Group also share this trait.

22. *Pronotum: angle*: **(0)** less than 50 degrees; **(1)** 50 degrees or greater.

Within the Mictis Group a steep pronotum is the norm: only *Mercennus gracilis*, both species of *Notobitopsis* and *Pternistria sexlineata* have a pronotal angle less than 50 degrees.

23. *Pronotum: texture*: **(0)** no prominent, irregular tubercles on surface; **(1)** prominent, irregular tubercles on surface.

The presence of prominent tubercles on the pronotum helps define the group of *Mictis profana, M. amboinensis, M. caja, M. tenebrosa, M. oceanensis* and *M. farinulenta*. This character is also shared by *Pternistria sexlineata*, the new species from Sumatra and *Mictis* serina.

24. *Pronotum: humeral angles*: **(0)** not extended; **(1)** extended slightly, less than width of head; **(2)** projecting outwards at least as wide as head.

In the Coreidae, the pronotum extends back, up and outwards into two lateral lobes or humeral angles. Within the Mictini the humeral angles of most taxa are extended at least slightly past the lateral margins of the abdomen. The lack of extended humeral angles unites *Mercennus gracilis* with *Pseudomictis* and *Notobitopsis*, whereas pronounced winglike projections join the two new species to *Priolonomiopsis amplicollis*, *Mictis pungens* to *M. formidabilis*, and *Molipterix hardwickii* to *Priolonomia gigas* and *Ochrochira pallsecens*. *Mictis farinulenta* also shows dramatic winglike humeral projections, which suggests that this taxon may be more closely related to *M. pungens* and *M. formidabilis* than is shown by this reconstruction. It also reminds us that this and many other characters probably have multiple origins with respect to these taxa.

25. *Pronotum: humeral angles*: **(0)** not applicable; **(1)** humeral angles narrowly pointed; **(2)** humeral angles produced into narrow spines; **(3)** humeral angles very broad.

Where present, the shape of the humeral extensions varies from narrow constricted points as in *Neomictis filicornis*, to narrowly tapered points as shared by *M. pungens* and *M. formidabilis* as well as the new species from Sarawak, to the more broad projections of most other taxa.

26. *Pronotum: humeral angles*: **(0)** not curved forwards; **(1)** curved forwards.

In some taxa the extended humeral angles are directed forwards, a condition that unites *Molipteryx hardwickii* with *Priolonomia gigas*, and is also seen in *Mictis farinulenta*.

27. *Pronotum: humeral angles*: **(0)** not curved upwards; **(1)** strongly curved upwards.

Humeral angles may also be angled sharply upwards. This character is shared by members of the Derepteryx Group including *Priolonomiopsis amplicollis*, both new species from Indonesia as well as *M. farinulenta*.

28. *Pronotum: humeral angles*: **(0)** angular or subacute; **(1)** rounded.

Rounded humeral angles unite *Mercennus gracilis* with *Notobitopsis* and *Pseudomictis*. In all other taxa sampled the humeral angles are either pointed or subacute.

29. *Pronotum: lateral margins*: **(0)** smooth or nodulose; **(1)** serrated; **(2)** strongly serrated.

Serrations along the lateral margins of the pronotum are seen in most of the taxa sampled. Smooth or smoothly nodulose lateral margins again unite *Mercennus gracilis* with *Pseudomictis* and *Notobitopsis*, as well as *Mictis serina* with *Xyrophoreus tonsor* and *Plectropoda bicolor* with *Elasmopoda* sp. *Mictis discolor* also has smooth lateral margins.

Thorax, lateral view (30 – 31) – On the lateral margins of the thorax, many taxa display unique colouration or setal patterning. Two distinct setal patterns were found to be phylogenetically useful and were coded as follows:

30. *Metathorax*: **(0)** no white pubescent patch; **(1)** white patch of pubescence above coxae.

Five of the species of *Mictis* in this study show a distinctive pale setal patch on the metathorax, directly above the hind coxa. In this analysis only four of these five species cluster together, yet despite this I believe that they are in fact more closely related (Fig. 2.11).

31. *Thorax: lateral line*: **(0)** no pubescent line along side of thorax; **(1)** white pubescent line along side of thorax.

A thick blond setal stripe running along the side of the thorax unites *Ochrochira pallescens* with *Priolonomia gigas*. Similar setal patterning is seen in several other taxa not available for this study, so the homology of this character throughout the Mictini is uncertain.

Characters of the scutellum:

Scutellum (32 – 33) – In all species examined the scutellum is laterally striated, and the apex is usually pale in colouration However, a small group of Asian taxa possess a distinct dark tubercle at its apex (O'Shea and Schaefer 1978). Two scutellar characters were coded as follows:

32. *Scutellum: apex*: **(0)** without tubercle; **(1)** with small tubercle.

Within the taxa studied, a small dark tubercle at the apex of the scutellum is autapomorphic for the genus *Molipteryx*, and thus does not contribute to the resolution of this phylogeny.

33. *Scutellum: apex*: **(0)** dark; **(1)** pale.

In virtually all taxa sampled the apex of the scutellum is pale in colouration. With only a few scattered species displaying a dark tip, this character is also of little phylogenetic value.

Characters of the male hindlimb:

Hindlimbs in the Mictini are generally sexually dimorphic, with males possessing incrassate and sometimes armed hind femora and ventrally armed hind tibiae. This dimorphism is believed to be under sexual selection, as male hindlimbs have been shown to function in male-male combat (e.g., Mitchell 1980, Miyatake 1997, Eberhard 1998). One must use caution in assessing the homology of characters that are potentially under strong selection. For example, Westlake *et al.* (2000) show that within the waterstrider genus *Rheumatobates* (Heteroptera: Gerridae), modifications of the male antennae and hindlimbs (used to subdue unwilling females during mating) have evolved more than once. However, in this case since there are so many either invariable or autapomorphic characters among the study species, one has little choice but to include these dimorphic traits. Nonetheless, there are a number of hind leg characters which have proven quite useful as phylogenetic characters, and are supported by other independent characters.

This is especially true for characters describing femoral shape and dorsal and ventral tibial dilations. Hindlimbs are illustrated in figures 2.12 and 2.13.

Hind femur (34 – 43) Ten characters of the hind femur were found to be potentially informative and were included in this analysis. These were coded as follows:

34. *Hind femur: dimorphism*: **(0)** not strongly sexually dimorphic; **(1)** strongly sexually dimorphic.

In most Mictini the male and female hind femora are strongly divergent, with the male femur being more incrassate and armed with various spines and tubercles, while the female hind femur is generally relatively unspecialized, though several have female-specific armature in the form of a terminal ventral fin-like spine. In some cases, female and male hindlimbs are more or less undifferentiated, with either both sexes expressing similar modifications, or neither sex expressing any significant modifications. Of these species, *Pternistria sexlineata*, both species of *Notobitopsis* and *Pseudomictis obtusispinus* share relatively non-dimorphic hindlimbs. Females of *Mercennus gracilis* and *Pseudomictis distinctus* were not available, but based on species descriptions their femora are apparently noticeably sexually dimorphic. *Mictis* serina and *Xyrophoreus tonsor* also share a lack of significant sexual dimorphism in femur shape, though this is probably symplesiomorphic. Several other taxa, *Mictis farinulenta, M. formidabilis, Neomictis filicornis* and *Aspilosterna acutangula* also show a lack of dimorphism.

35. *Male hind femur: base*: **(0)** femur thick at trochanter; **(1)** femur thin at trochanter.

Where the hind femur joins the trochanter the femur may either be fairly thin or quite robust in structure, with a thickened junction being common to members of the

Derepteryx Group as well as the group of *Mercennus gracilis, Notobitopsis, Pseudomictis* and *Pternistria sexlineata*. In all other taxa the femur is fairly thin at its base, in most cases appearing stalked.

36. *Male hind femur: curvature*: **(0)** hind femur straight or evenly curved throughout; **(1)** hind femur with a distinct bend.

All taxa sampled have at least somewhat curved femora, though there are a few species where the hind femur is only minimally angled. In some cases it is uncertain whether this lack of curvature reflects the normal condition, or whether the specimens sampled are simply small males which exhibit secondary sexual traits to a lesser degree than their larger brethren (for a further discussion of scaling relationships of sexual characters see Chapter 3). This may be the case for the single specimen of *Mictis farinulenta*, for example. In other cases such as the Derepteryx Group, lack of femoral curvature appears to be a genuine character linking them together.

37. *Male hind femur: incrassate*: **(0)** femur thin, not greatly incrassate; **(1)** femur with distinct incrassate bulge after bend; **(2)** femur incrassate throughout its entire length.

Males of most of the taxa sampled have strongly incrassate hind femora. *Mercennus gracilis, Notobitopsis* and *Pseudomictis* are united by the possession of an even enlargement of the femur running its whole length, a condition also seen in *Molipteryx hardwickii* and *Ochrochira pallescens*. In most other taxa the femur begins with a thin petiole or stalk, with the femur only becoming incrassate after the stalk. Very thin and minimally swollen hind femora occur in a few taxa. As above this condition is unclear for *Mictis farinulenta*, while in *Aspilosterna acutangula*, *Priolonomiopsis amplicollis* and *Priolonomia gigas* this is certainly the typical condition expressed by males.

38. *Male hind femur: stalk at base*: **(0)** not applicable; **(1)** relatively short but distinct section prior to bend in femur; **(2)** long, thin section before bend in femur.

In those species where the femur is stalked at the base, this stalk may be either short or long – a distinction which helps to divide the genus *Mictis* into roughly two discrete groups: *M. profana*, *M. amboinensis*, *M. caja*, *M. tenebrosa*, *M. oceanensis*, and *M. longicornis*, *M. gallina*, *M. pungens*, *M. formidabilis* plus *Neomictis filicornis*. Other taxa with a short stalked base include both African species, *Priolonomiopsis amplicollis* plus the two undescribed species, *Mictis* serina *and Aspilosterna acutangula.* Of the remaining taxa, *Xyrophoreus tonsor* displays a long stalk and general hind femur structure very similar to that of *Neomictis filicornis*.

39. *Male hind femur: texture*: **(0)** more or less smooth or evenly textured; **(1)** with uneven longitudinal rows of large tubercles.

Uneven rows of tubercles along the lateral margins of the hind femur are shared by *Mercennus gracilis* and *Pternistria sexlineata*, as well as males of the Derepteryx group, with those species in the Derepteryx group showing much larger tubercles and spines.

40. *Hind femur ventral spines*: **(0)** without large conical ventral spines; **(1)** with large, conical ventral spines.

In addition to rows of large femoral tubercles, *Molipteryx hardwickii*, *Priolonomia gigas* and *Ochrochira pallescens*, also share distinct, large conical spines on the ventral margin of the femur.

41. *Male hind femur: ventral margin*: **(0)** without prominant ventral serrate bulge; **(1)** with prominent ventral serrate bulge, near apex.

On the ventral margin of the hind femur, *Pseudomictis distinctus*, *Pternistria sexlineata* and both African species *Plectropoda bicolor* and *Elasmopoda* sp. have a unique curved serrate bulge not seen in the other taxa. When viewed ventrally this structure is quite distinctive, and is considered to be one of several fairly strong characters uniting the two Plectropoda Group members with these and other Asian species.

42. *Male hind femur: articulation at trochanter*: **(0)** trochanter articulates at tip of femur; **(1)** trochanter articulates below the end of the femur.

Only in *Mercennus gracilis* does the hind trochanter insert below the end of the femur. This character is taxonomically useful though it is of no use in this phylogenetic reconstruction.

43. *Hind femur: dorsal margin*: **(0)** none ; **(1)** dorsal dilation.

A dorsal dilation along the hind femur is seen in a few taxa, but since they are not clustered together in this phylogeny, I consider this trait to be reflective of parallel evolution rather than homology.

Hind tibia (44 – 50) Within the Mictini, several characters of the hind tibia are quite useful in determining relationships. In all the species sampled, males possess a ventral tibial spine, which is sometimes expanded into a leaf-like dilation. As well, some taxa also have a dorsal tibial dilation. Seven hind tibial characters were coded as follows:

44. *Hind tibia: ventral spine*: **(0)** no ventral spine ; **(1)** ventral spine 1/3 down ; **(2)** ventral spine 1/2 way down; **(3)** ventral spine 2/3 down.

The location of the hind tibial spine is very useful in defining clades in this study. Within the genus *Mictis*, several differences in hindlimb structure contribute to the division of the genus into two discrete clades. This is also one of a suite of characters tying *Priolonomiopsis amplicollis* to the new species from Sumatra.

45. *Male hind tibia: dorsal dilation*: **(0)** little or no dilation; **(1)** pronounced, simple leaf-like dilation; **(2)** wavy dilation flaring out at the apex.

Elaborately-shaped dorsal tibial dilations are especially useful in establishing the relationship between the two African species and *Mercennus gracilis, Pternistria sexlineata* and the genus *Pseudomictis*. In this region of the tree only the genus *Notobitopsis* lacks this distinctive feature. A leaf-like dilation running the full length of the tibia also unites the new species from Sumatra with *Priolonomiopsis amplicollis*.

46. *Male hind tibia: dorsal sub-apical margin* : **(0)** no dorsal sub-apical teeth; **(1)** 2 or more sub-apical teeth on dorsal margin of tibia.

Along the dorsal margin of the hind tibia right near the apex several species show two or more minute teeth. Incidentally, this feature is shared by all of the taxa possessing the blond metathoracic setal patch (character 30), and is further evidence that these species may be even more closely related than this phylogenetic reconstruction implies.

47. *Male hind tibia: ventral spine*: **(0)** ventral spine simple, if dilated then only at spine; **(1)** narrow dilation down to spine, then sharply constricted to end; **(2)** ventral dilation irregular and wavy, running the whole length: one spine 2/3 down and another at end; **(3)** ventral dilation continuing above and below the tibial spine.

The ventral tibial spine is quite variable in form. In the genus *Mictis* this spine is either simple and spine-like or larger and leaflike. In either case, the ventral tibial dilation (if there is one) does not continue below the spine. The Derepteryx Group, *Apsilosterna acutangula* and the genus *Notobitopsis* also have leaf-like ventral dilations with the dilation ending at the spine. *Mictis* serina and *Xyrophoreus* share simple undilated spines, whereas *M. discolor* has a small serrated and dilated spine unlike any other. Tibial spine and dilation shape is most useful in uniting *Mercennus gracilis*, *Pseudomictis* and *Pternistria sexlineata* with the African Plectropoda Group. The new species from Sarawak also appears to share these tibial features, albeit in a much reduced fashion. A large, leaf-like spine running the full tibial length is shared by *Priolonomiopsis amplicollis* and the undescribed species from Sumatra.

48. *Male hind tibia: ventral serrations above spine*: **(0)** none; **(1)** serrate or nodulose from base down to tibial spine.

Notobitopsis, *Pseudomictis*, *Pternistria sexlineata* and *Elasmopoda* sp. are all united by the possession of ventral tibial serrations or nodules running from the top of the tibia down to the tibial spine.

49. *Male hind tibia: ventral serrations below spine*: **(0)** no serrations below spine; **(1)** distinctly serrate or toothed below tibial spine.

Ventral tibial serrations below the spine are shared by many species. Within *Mictis*, most of the species are united by this feature, as is the Derepteryx Group.

50. *Male hind tibia: curvature*: **(0)** not curved ; **(1)** curved inwards.

In most species the hind tibia is deflected ventrally at the tibial spine. A lack of such curvature links *Priolonomiopsis amplicollis* and the two new species with the group of species associated with the two African taxa. Within this grouping only the genus *Notobitopsis* and *Pseudomictis obtusispinus* have curved hind tibiae.

Body shape and colouration:

When viewed from above, male body shape is sometimes useful in grouping taxa together. Colouration is also sometimes useful, though non-structural characters should always be used with caution because of the high potential for convergence. Three characters describing shape and three describing various aspects of body colour were coded as follows:

Body shape (51 – 53)

51. *Male body shape*: **(0)** not as below; **(1)** broad at humeral angle, then curved in and tapered; **(2)** long and narrow.

Male body shape is generally the same throughout the taxa, though narrow body shape helps to delineate some groups. *Mictis discolor*, *M. longicornis*, *M. gallina* and *Neomictis filicornis* all have long, narrow abdomens, as do the African species and those Asian taxa most closely related to them. Additionally, *Plectropoda bicolor* and *Pternistria sexlineata* are exceptionally broad across the metathorax, then taper in towards the end of the abdomen.

52. *Abdominal segment VI*: **(0)** not flared; **(1)** flared.

Both *Elasmopoda* and *Plectropoda bicolor* show lateral flaring of abdominal segment VI. This character supports the strong relationship between these two species, but does little to relate these to any of the other included taxa.

53. *Abdomen: lateral margins*: **(0)** smooth or finely nodulose; **(1)** weakly spined ; **(2)** strongly spined.

Weak lateral spines along the lateral margins of the abdomen occur in several unrelated taxa, but is useful in uniting *Mictis profana, M. amboinensis* and *M. caja*. Stronger lateral spines are seen in *Mercennus gracilis* and *Pternistria sexlineata*, and may reflect an even closer relationship than shown in this study.

Colouration (54 – 56)

54. *Hemelyra: dorsal colouration*: **(0)** not speckled; **(1)** speckled.

Although characters associated with superficial colouration are often considered to be weak characters which may be easily gained and lost, the speckled patterning along the hemelytra of the Derepteryx Group would appear to be apomorphic for this group. This colouration is also shared by *Aspilosterna acutangula* and may reflect a closer relationship among them.

55. *Hemelytra*: *dorsal colouration*: **(0)** no coloured cross; **(1)** coloured cross on hemelytra and trailing edges of scutellum.

The coloured cross that helps to link *Mictis amboinensis* to *M. profana* is likely convergent with that displayed in *Notobitopsis militaris* and *Plectropoda bicolor*. Between *M. profana* and *M. amboinensis* the strength of this cross is virtually the only difference between the two taxa, suggesting that the latter may in fact be merely a subspecies of the former.

56. *Abdomen: dorsal colouration*: **(0)** abdomen all orange/red (may have some black markings); **(1)** dark blue/ brown with two pale lateral spots; **(2)** yellow or orange with black/brown line running longitudinally the full length (central line may be joined to lateral margins with dark markings); **(3)** banded orange and black.

Despite claims to the opposite (O'Shea 1975), adult Mictines are strongly aposematic, as evidenced by the bright abdominal colouration revealed when they take to the wing. This colouration is variable throughout the Mictini, though in general most taxa exhibit an orange or red abdomen, occasionally with some brown or black lateral or medial patterning. A yellow or orange abdomen with a dark brown or black longitudinal stripe running down the middle is shared by *Elasmopoda* sp., *Xyrophoreus tonsor* (in *X. tonsor* this is accompanied by dark markings joining the central dark band with the lateral margins) and *Neomictis filicornis*, yet these species do not appear closely related. The abdomen of *Mictis caja* is banded orange and black as a wasp, a condition not seen in other taxa sampled. The unique colouration of *M. tenebrosa* and *M. gallina* - a dark abdomen with two pale lateral spots as seen in some other wasp-mimics (see figure 2.14), suggests that these two taxa may be more closely related than this reconstruction implies.

Female hindlimb structure:

Many female morphological traits are either consistent and uninformative, or else appear to be linked to the male characters. Female hindlimbs, however, have been found in some cases to express characters that are not present in the male and are therefore assumed to be independent. One female hindlimb character was coded as follows:

Female hind tibia –

57. *Hind tibia: female*: **(0)** straight ; **(1)** with distinct ventral bulge ; **(2)** with ventral leaf-like dilation ; **(3)** with ventral and dorsal leaf-like dilations.

Only one female-specific character is included in this study. A distinct ventral bulge along the upper margin of the hind tibia unites approximately half of the genus *Mictis*, with the other half unmodified. This character is also shared by both species of *Notobitopsis*. In one species, *Priolonomia gigas*, females also possess a ventral leaf-like dilation, while in *Pseudomictis*, *Pternistria* and *Plectropoda bicolor* both ventral and dorsal dilations are present. Unfortunately, females of several females were not available, resulting in gaps in the dataset.

Ventral abdominal characters:

As well as possessing sexually dimorphic hindlimbs, the males of many Mictini have ventral abdominal tubercles and spines, which function in courtship and perhaps combat as well (Chapters 4 and 5). Again, these characters should be viewed with caution, as they are probably under strong selection and so could show patterns inconsistent with the true phylogeny. Although the presence and absence of an elaborate structure is typically thought of as a strong character, studies of scaling relationships between tubercles and body size in *Mictis profana* (Chapter 3) reveal that small males may have almost non-existent median tubercles, and in extreme cases this could influence coding. It is in fact conceivable that some males might altogether forego the production of these secondary sexual structures, perhaps due to environmental constraints during development. In a series of museum specimens of *Mictis longicornis* from Java, for example, several small males completely lacked the large median tubercle typical of the species. Likewise there are two specimens of *Mercennus gracilis* at the British Museum, the larger one with enormous paired ventral spines, and the smaller with no tubercles whatsoever. All other characters, including genitalia, appear identical. Bearing this in mind, *Xyrophoreus tonsor*, which is described as lacking a median tubercle (P'Shea and Schaefer 1980), does in fact have a small but distinct tubercle and is therefore coded as such. Ventral abdominal characters of most species are illustrated in figure 2.15. Abdominal characters for the undescribed species from Sumatra (= *Priolonomiopsis sumatra*) and Sarawak (= *P. sarawaensis*) are illustrated in figures 2.18 and 2.19 respectively. Seven male ventral abdominal characters were coded as follows:

Lateral tubercles (58 – 59)

58. *Abdomen: ventrolateral tubercles*: **(0)** no lateral tubercles or spines; **(1)** lateral tubercles or spines on III in males; **(2)** lateral tubercles or spines on III and IV in males.

Almost all taxa in this study possess lateral abdominal tubercles on abdominal segment III. *Pternistria sexlineata, Elasmopoda* sp. and *Plectropoda bicolor* also possess lateral tubercles on segment IV, while the new species from Sumatra and

Priolonomiopsis amplicollis are joined by their lack of any lateral tubercles, a condition also shared by *Mictis formidabilis*, *Mercennus gracilis*, *Molipteryx hardwickii* and *Priolonomia gigas*.

59. *Abdomen: ventrolateral tubercles*: **(0)** inapplicable; **(1)** located wide apart on sides of segment III; **(2)** located on the median abdominal tubercle.

For those taxa possessing ventrolateral tubercles, these are typically spaced fairly widely apart, well before the base of the median abdominal tubercle (when present). In *Neomictis filicornis* however, the lateral tubercles are mounted directly upon the median tubercle itself, a condition seen in no other species.

Median abdominal tubercles (60 – 62)

60. *Median abdominal tubercle*: **(0)** no median tubercle or raised ridge; **(1)** margin of III and IV raised into a ridge; **(2)** median tubercle(s) present.

Presence of one or more median abdominal tubercles on the margin of abdominal segments III and IV separates most taxa from the Derepteryx Group species *Molipteryx hardwickii*, *Ochrochira pallescens* and *Priolonomia gigas*. *Priolonomiopsis amplicollis* possesses two median tubercles, and this character along with several other help to remove this species from the abovementioned group. Within the genus *Mictis*, only *M. discolor* and *M. gallina* lack a median tubercle or raised ridge (however the latter has so many other characters in common with *M. longicornis* that in this case this is assumed to reflect a loss of this trait). Though lacking a full tubercle, both species of *Notobitopsis* have a distinct raised ridge along the margin of the two segments. In *Aspilosterna acutangula* the median tubercle is expressed as a nodulose incrassate bulge in the middle of segment IV, which is unique and may or may not be homologous with the tubercles of other species.

61. *Abdominal segments III and IV*: **(0)** inapplicable; **(1)** median tubercle not cleft; **(2)** median tubercle cleft; **(3)** median tubercle divided into two spines or tubercles side-by-side.

Where a median tubercle is present it is frequently cleft with a longitudinal furrow which in some cases may be quite deep. This character lends further support for the division of *Mictis* into two clades, but elsewhere in the phylogeny it appears to have arisen multiple times. This groove is used in at least two species (*Mictis profana* and *M. tenebrosa*) during courtship, whereby the male lowers this cleft into contact with the lateral margin of the female's abdomen and rubs it back and forth (discussed in Chapter 4). If other species court in a similar manner, then the multiple development of this cleavage, which may act as a sort of guide, is unsurprising.

In *Mercennus gracilis, Pternistria sexlineata, Pseudomictis distinctus, Plectropoda bicolor* and *Elasmopoda* sp., the median tubercle is completely cleft to the point where it is now divided into two distinct tubercles side by side.

62. *Margin of abdominal segments III and IV*: **(0)** not extended caudally; **(1)** extended somewhat caudally; **(2)** extended caudally, median tubercle emerges out of segment V.

In most of the species with either a median tubercle or a raised lip on the margin of segments III and IV, this margin is directed somewhat caudally. In a few cases, the trailing edges of both segments III and IV are extended backward, with the median tubercle(s) emerging out of the caudal margin of segment V. This last state is considered to be strong support for a close relationship between both species of *Pseudomictis* and *Plectropoda bicolor*.

Ventral abdominal texture (63)

63. *Ventral surface of abdomen*: **(0)** smooth; **(1)** tuberculate.

Mictis amboinensis, M. profana, M. caja, M. tenebrosa and M. oceanensis are all united by the possession of numerous small tubercles covering the ventral surface of the abdomen, as are *Mercennus gracilis, Notobitopsis, Pseudomictis* and *Pternistria sexlineata*. This feature is also seen in the undescribed species from Sarawak.

64. *Abdominal segment VI*: **(0)** no tuberculate bulge; **(1)** small tuberculate bulge on caudal margin.

The final character in this analysis, a small tuberculate bulge on the caudal end of abdominal segment VI is seen in *Mercennus gracilis* and *Xyrophoreus tonsor*. In the present reconstruction this character has arisen more than once (or has been lost in several taxa), and thus provides us with little phylogenetic information.

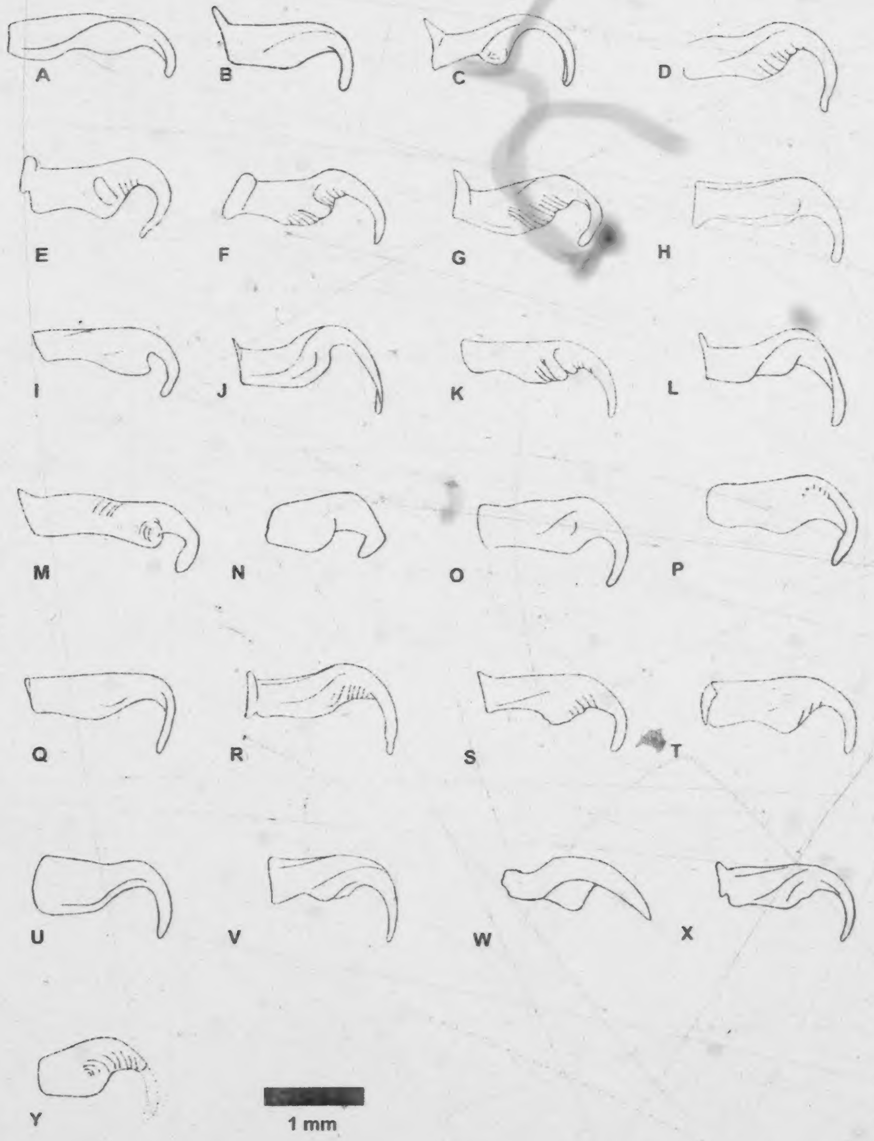


Figure 2.3. Parameres of the Mictini. A) *Mictis profana* (= *M. amboinensis*); B) *M. caja*; C) *M. farinulenta*; D) *M. pungens*; E) *M. longicornis*; F) *M. gallina*; G) *M. tenebrosa*; H) *M. serina*; I) *M. discolor*; J) *Xyrophoreus tonsor*; K) *Neomictis filicornis*; L) *Aspilosterna acutangula*; M) *Notobitopsis aruana*; N) *Mercennus gracilis*; O) *Pseudomictis distinctus*; P) *P. obtusispinus*; Q) *Pternistria sexlineata*; R) *Priolonomiopsis amplicollis*; S) *Priolonomia gigas*; T) *Molipteryx hardwickii*; U) *Ochrochira pallescens*; V) *Plectropoda bicolor*; W) *Elasmopoda* sp.; X) new sp. from Sumatra; Y) new sp. from Sarawak (tip damaged during dissection.)

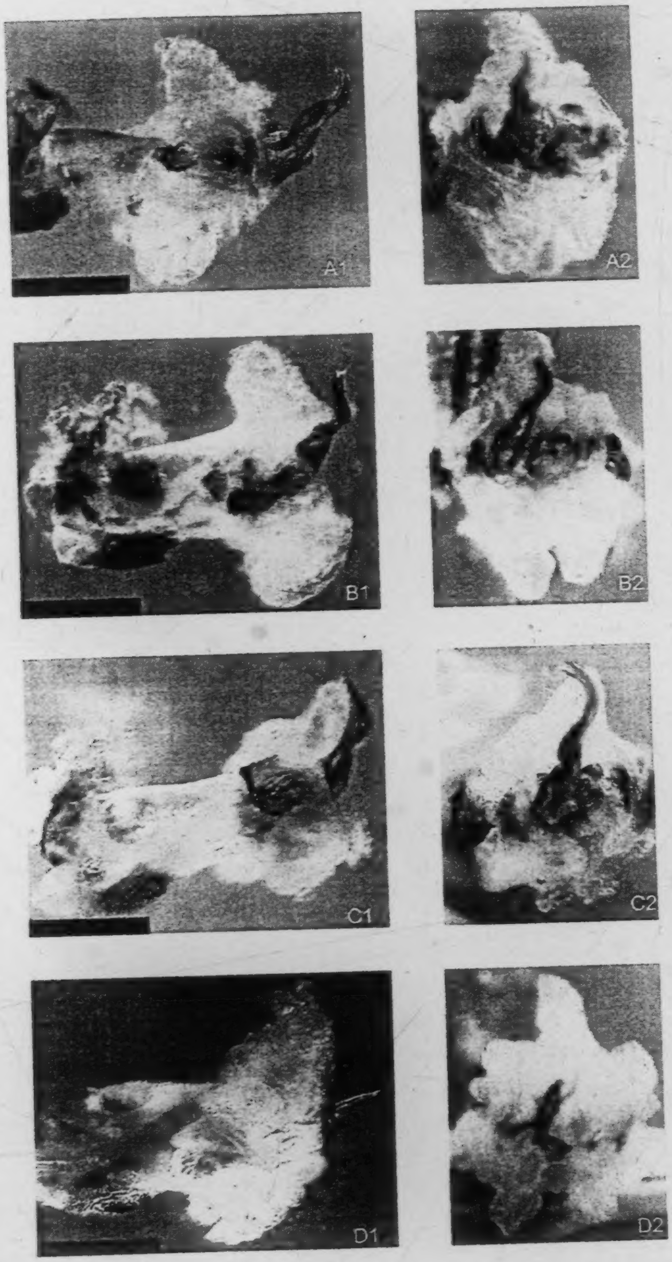

A1
A2
B1
B2
C1
C2
D1
D2

Figure 2.4. Aedeagus, lateral (1) and frontal (2) views: A) *Mictis profana*, B) *M. amboinensis*, C) *M. caja*, D) *M. pungens*. Scale bar indicates 1 mm.

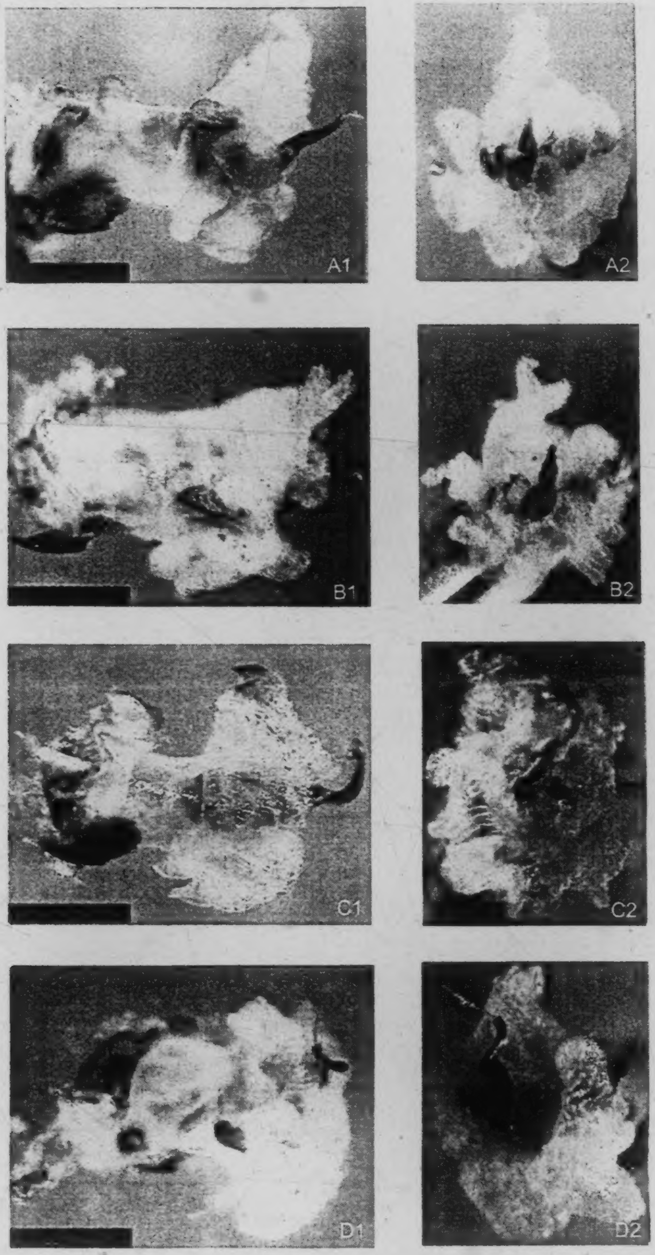

A1
A2
B1
B2
C1
C2
D1
D2

Figure 2.5. Aedeagus, lateral (1) and frontal (2) views: A) *Mictis longicornis*, B) *M. gallina*, C) *M. discolor*, D) *M. farinulenta*. Scale bar indicates 1 mm.

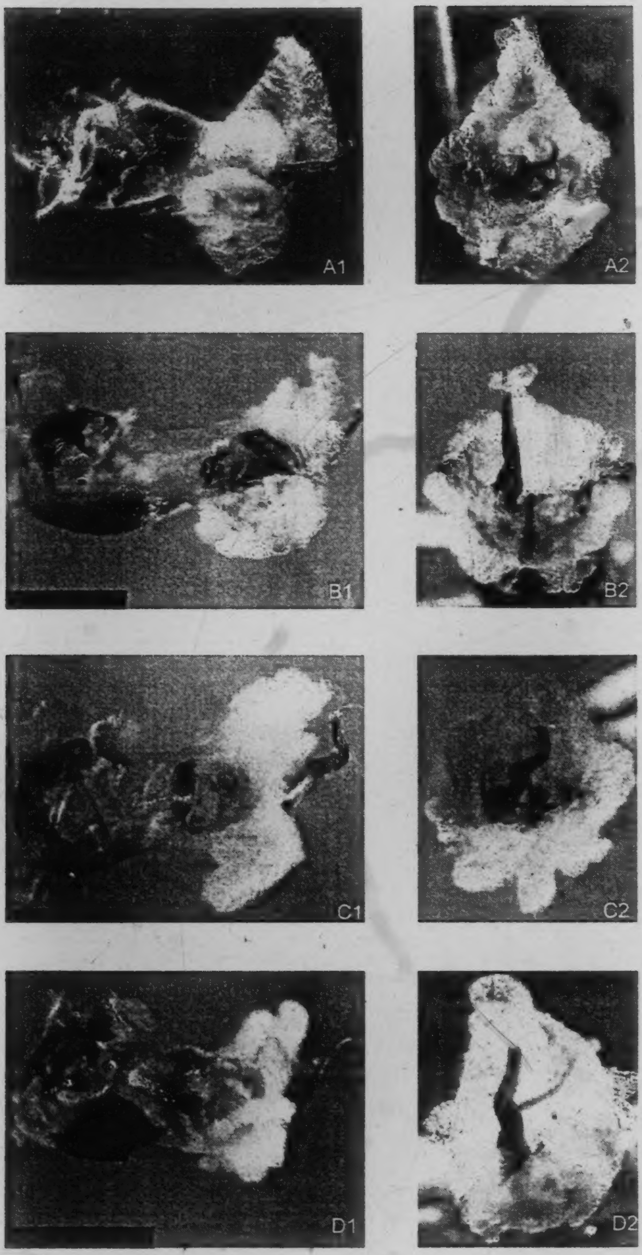

A1
A2
B1
B2
C1
C2
D1
D2

Figure 2.6. Aedeagus, lateral (1) and frontal (2) views: A) *Mictis* serina, B) *M. tenebrosa*, C) new sp. from Sarawak, D) new sp. from Sumatra. Scale bar indicates 1 mm.

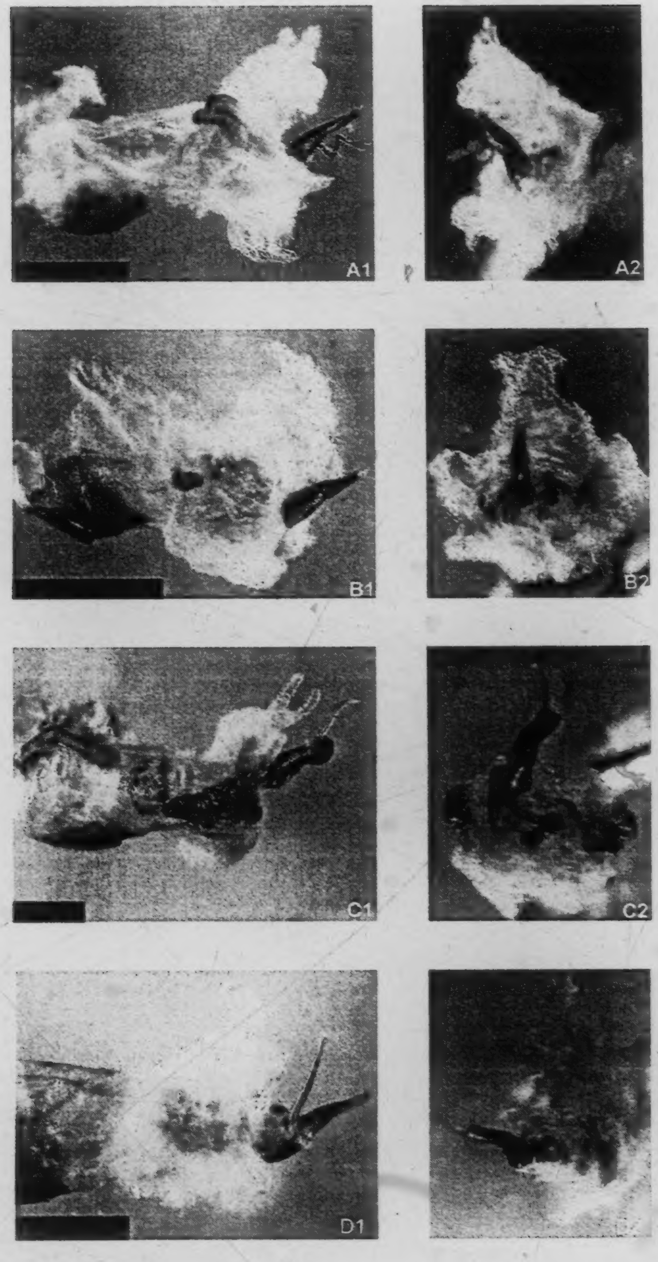


Figure 2.7. Aedeagus, lateral (1) and frontal (2) views: A) *Aspilosterna acutangula*, B) *Xyrophoreus tonsor*, C) *Mercennus gracilis*, D) *Neomictis filicornis*. Scale bar indicates 1 mm.

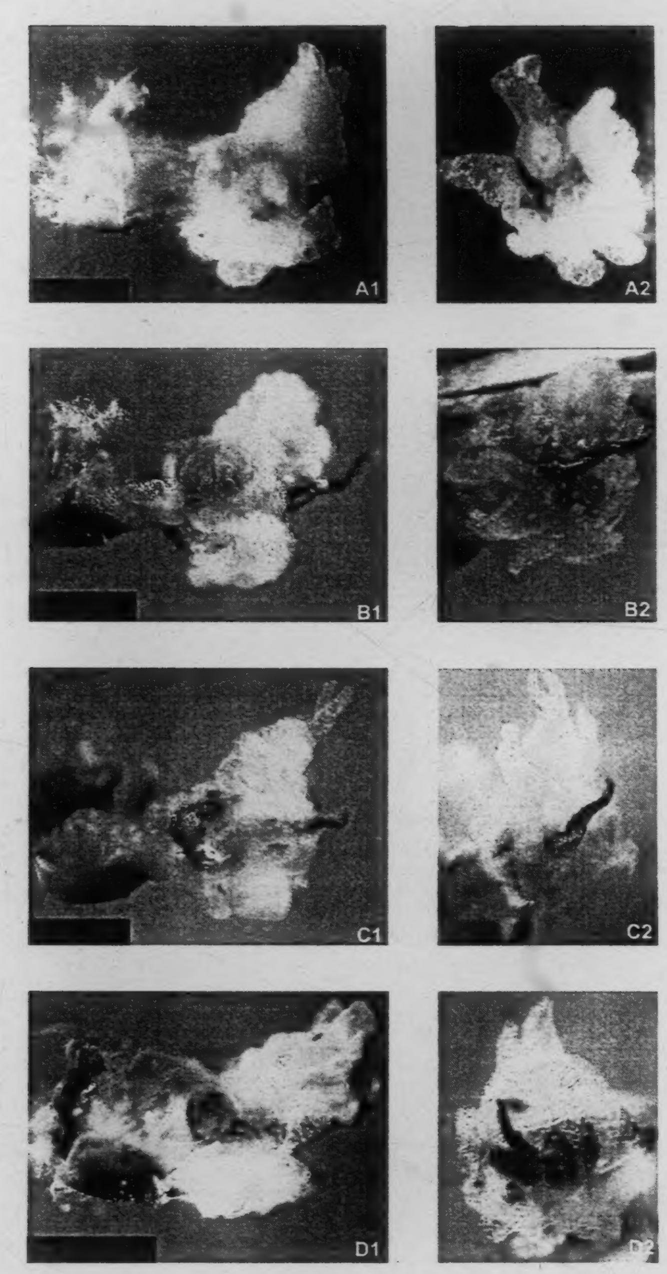

A1
A2
B1
B2
C1
C2
D1
D2

Figure 2.8. Aedeagus, lateral (1) and frontal (2) views: A) *Priolonomia gigas*, B) *Molipteryx hardwickii.*, C) *Pternistria sexlineata*, D) *Elasmopoda* sp. Scale bar indicates 1 mm.

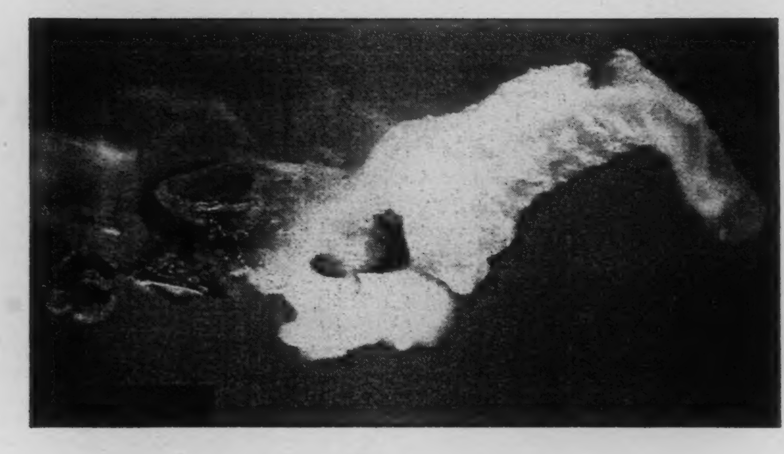


Figure 2.9. Aedeagus, lateral view: *Notobitopsis aruana*. Scale bar indicates 1 mm.

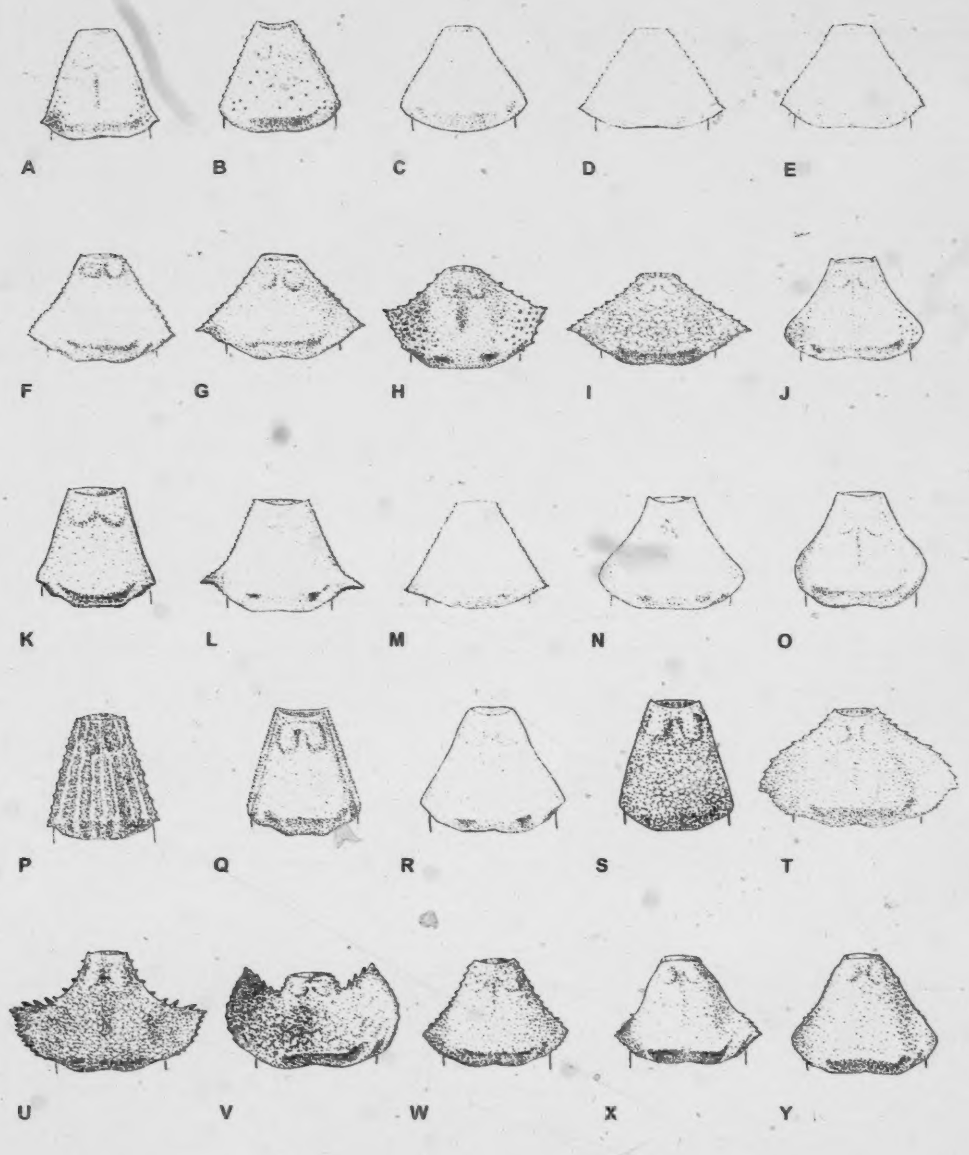


Figure 2.10. Pronotum, dorsal view: A) *Mictis profana* (~ *M. amboinensis*), B) *M. caja*, C) *M. tenebrosa*, D) *M. longicornis*, E) *M. gallina*, F) *M. oceanensis*, G) *M. pungens*, H) *M. farinulenta*, I) *M. formidabilis*, J) *M.* serina, K) *M. discolor*, L) *Neomictis filicornis*, M) *Aspilosterna acutangula*, N) *Pseudomictis distinctus*, O) *P. obtusispinus*, P) *Pternistria sexlineata*, Q) *Notobitopsis aruana* (~*N. militaris*), R) *Xyrophoreus tonsor*, S) *Mercennus gracilis*, T) *Priolonomiopsis amplicollis*, U) *Priolonomia gigas*, V) *Molipteryx hardwickii*, W) *Ochrochira pallescens*, X) *Elasmopoda* sp., Y) *Plectropoda bicolor*.

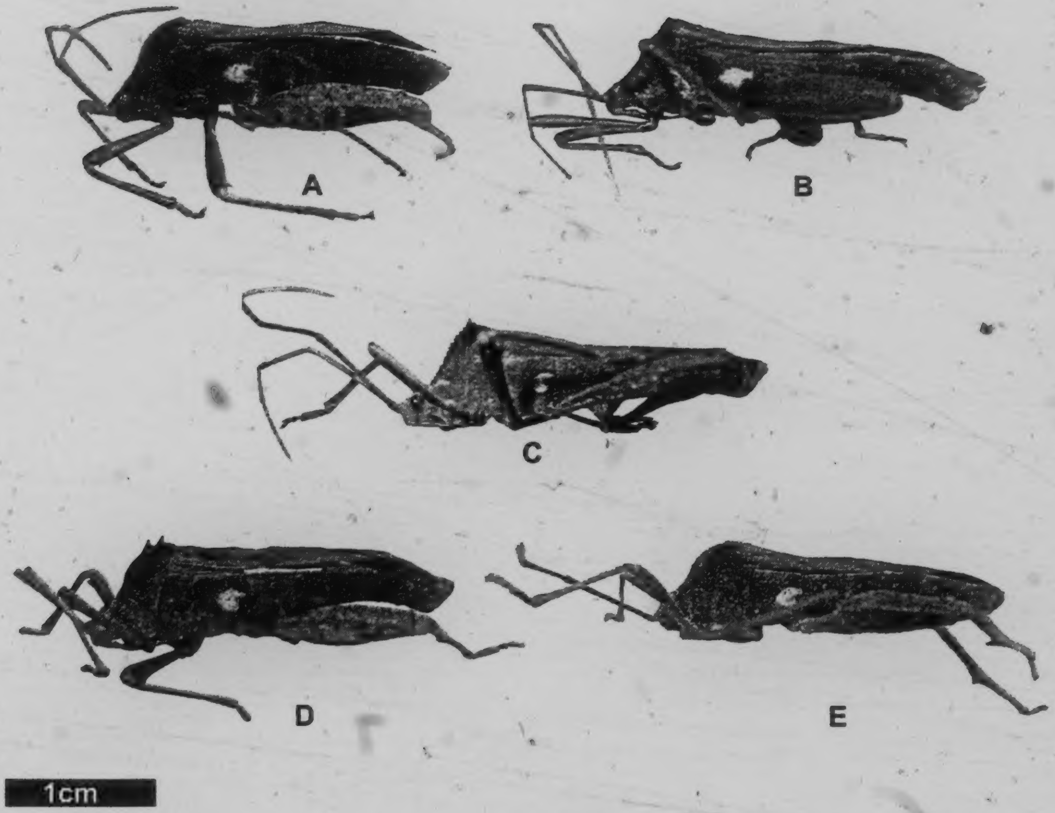


Figure 2.11. Metathoracic setae. A distinctive blond pubescent patch on the metathorax is seen in A) *Mictis tenebrosa*, B) *M. longicornis*, C) *M. formidabilis*, D) *M. pungens* and E) *M. gallina*. This structure suggests a close affinity between these species.

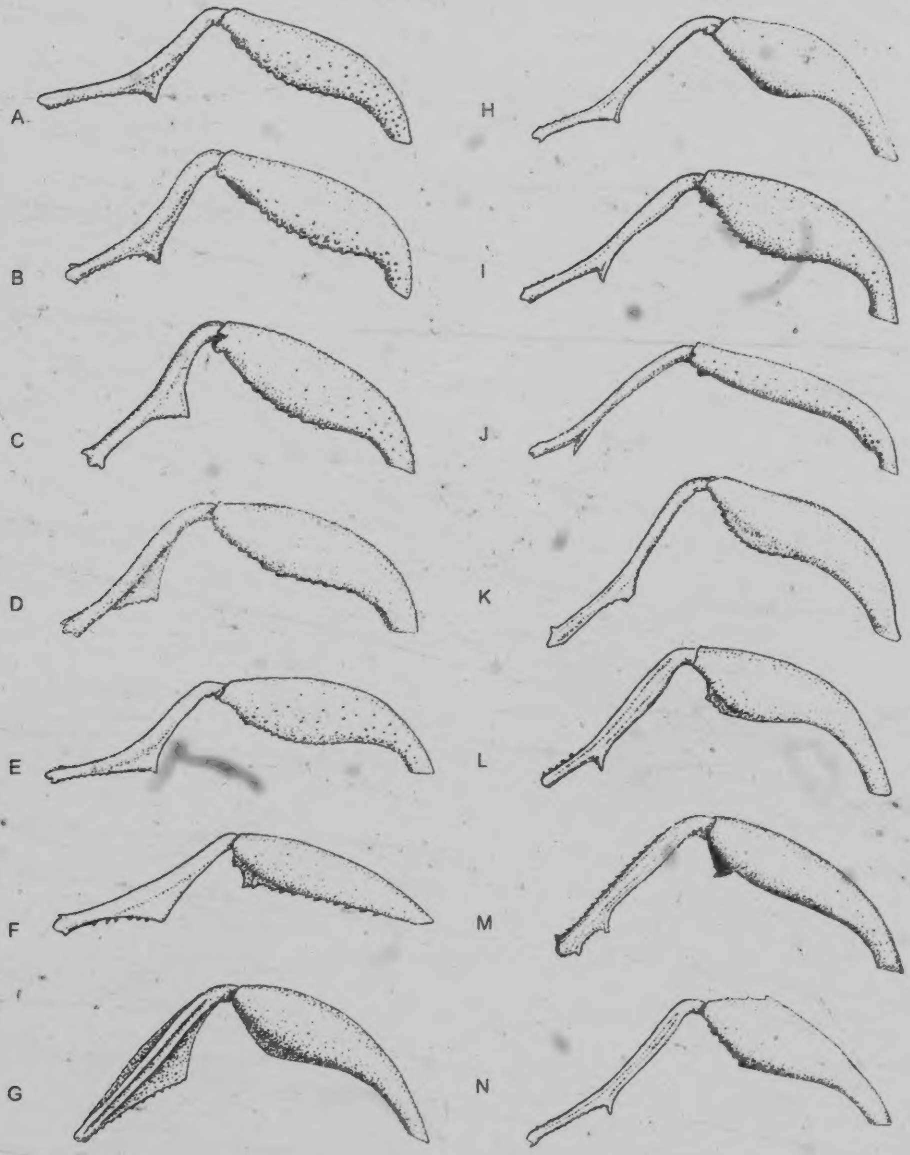


Figure 2.12. Lateral view of male hindlimbs: A) *Mictis profana*; B) *M. amboinensis*; C) *M.caja*; D) *M. oceanensis*; E) *M. tenebrosa*; F) *M. farinulenta*; G) *M. formidabilis*; H) *M. gallina*; I) *M. longicornis*; J) *M.* serina; K) *M. discolor*; L) *M. pungens*; M) undescribed species from Sarawak; N) *Neomictis filicornis*.

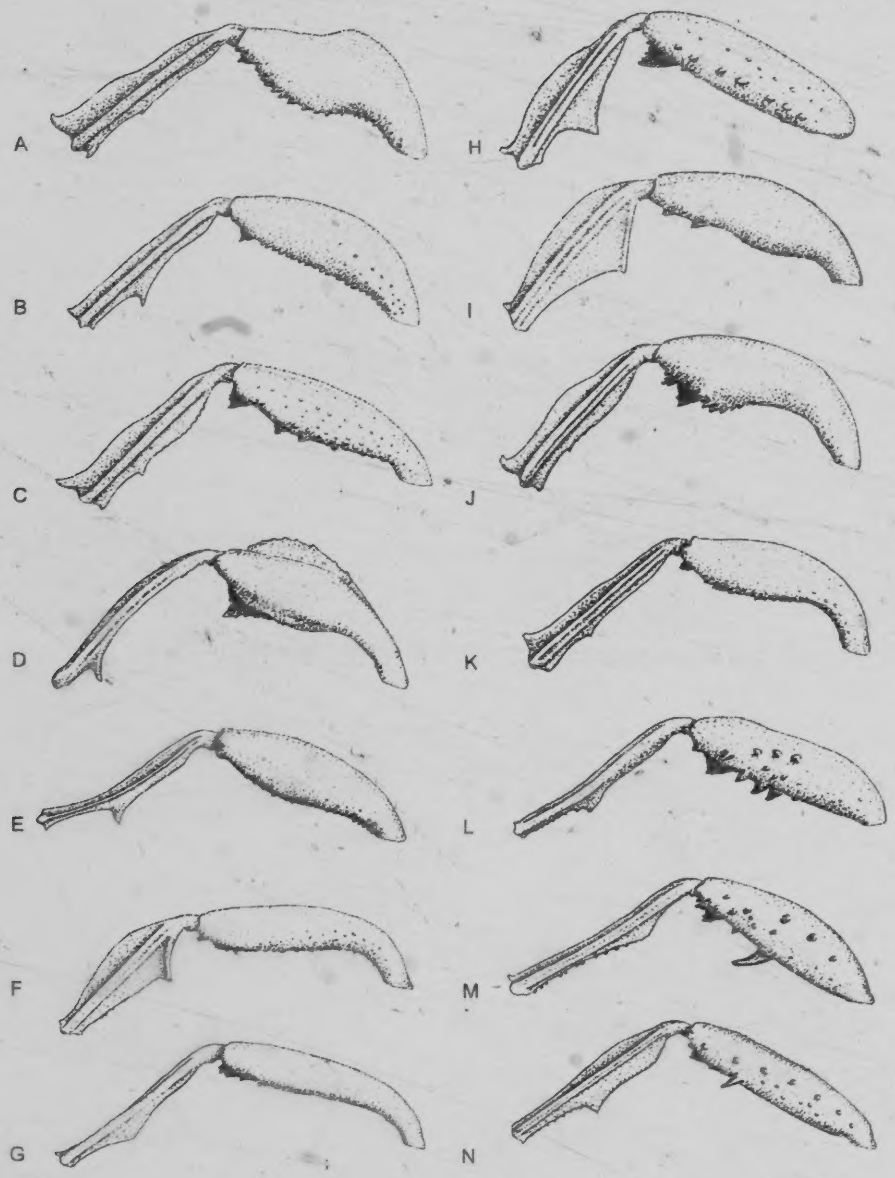


Figure 2.13. Lateral view of male hindlimbs (cont.): A) *Pseudomictis distinctus*; B) *P. obtusispinus*; C) *Pternistria sexlineata*; D) *Xyrophoreus tonsor*; E) *Notobitopsis aruana*; F) *Priolonomiopsis amplicollis*; G) *Aspilosterna acutangula*; H) *Mercennus gracilis*; I) undescribed species from Sumatra; J) *Elasmopoda sp.*; K) *Plectropoda bicolor*; L) *Molipteryx hardwickii*; M) *Ochrochira pallescens*; N) *Priolonomia gigas*.

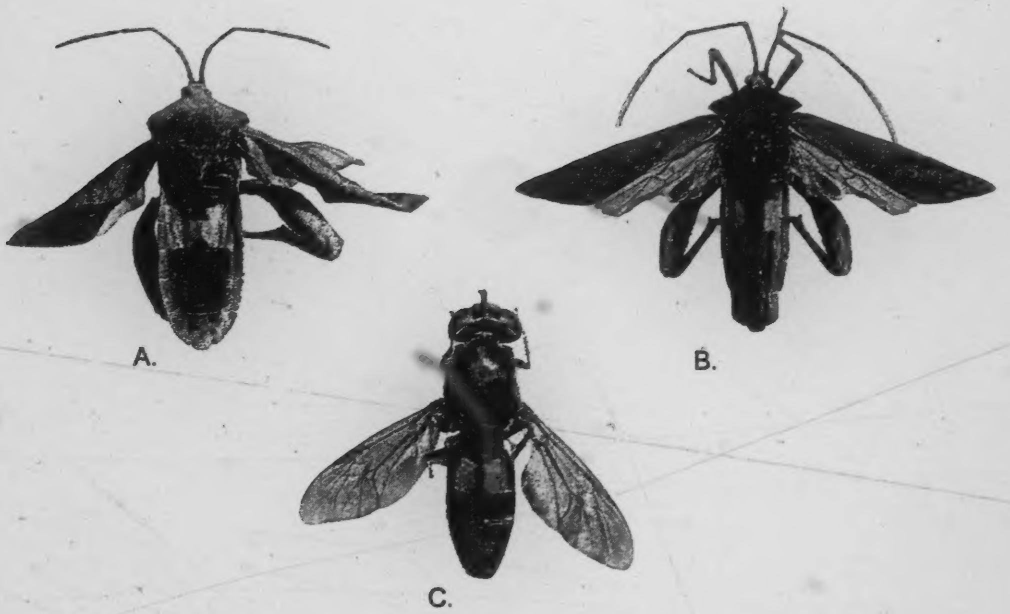


Figure 2.14. A comparison of mimetic patterning in *Mictis tenebrosa* (A), *M. gallina* (B) and an unidentified soldier fly (Diptera: Stratiomyidae) from West Kalimantan (C). Paired pale "windows" create the effect of a thread-waist as in many Hymenoptera. Additionally, when alive the dorsal abdominal colouring of *M. tenebrosa* is a brilliant metallic blue, similar to many tropical sphecoid wasps.

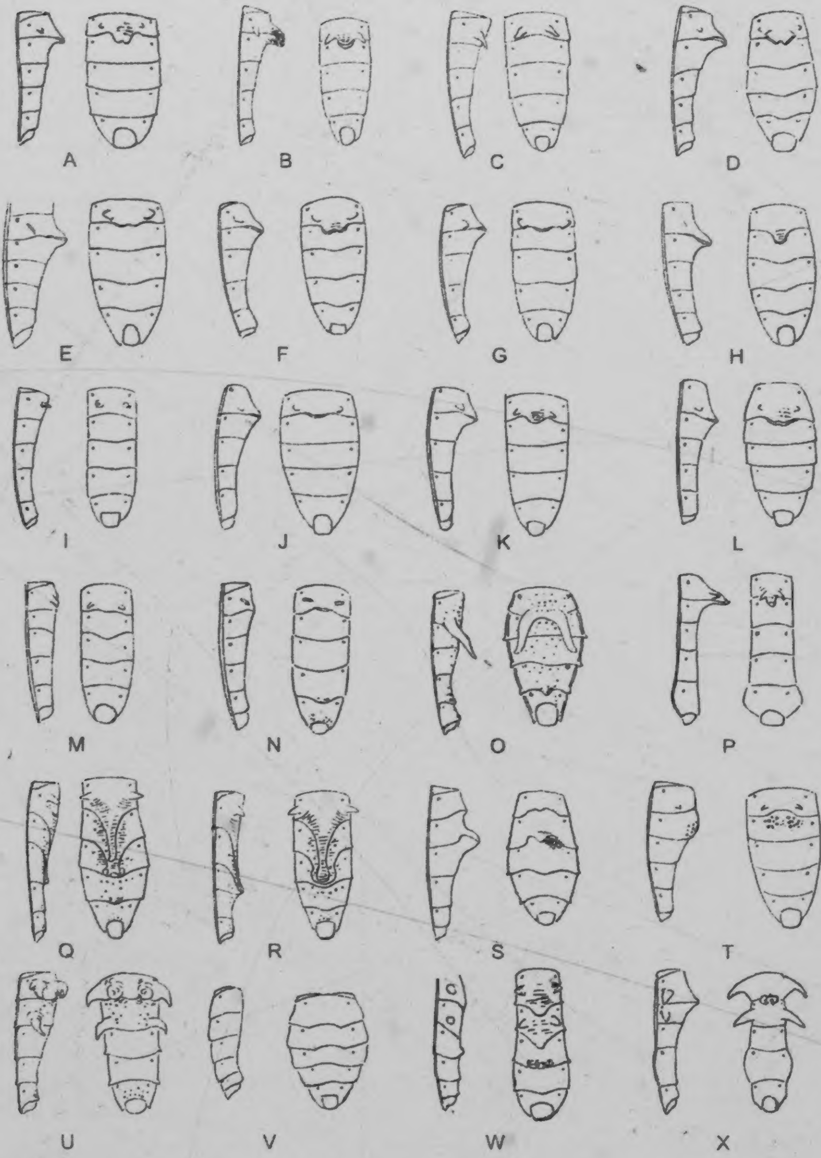


Figure 2.15. Ventral and lateral views of male abdomens: A) *Mictis tenebrosa*; B) *M. longicornis*; C) *M. gallina*; D) *M. serina*; E) *M. profana*; F) *M. oceanensis*; G) *M. amboinensis*; H) *M. formidabilis*; I) *M. discolor*; J) *M. farinulenta*; K) *M. pungens*; L) *M. caja*; M) *Notobitopsis aruana*; N) *Xyrophoreus tonsor*; O) *Mercennus gracilis*; P) *Neomictis filicornis*; Q) *Pseudomictis distinctus*; R) *P. obtusispinus*; S) *Priolonomiopsis amplicollis*; T) *Aspilosterna acutangula*; U) *Pternistria sexlineata*; V) *Molipteryx hardwickii*; W) *Plectropoda bicolor* X) *Elasmopoda* sp.

Phylogenetic Analysis

Through heuristic searching, six equally most parsimonious trees (MPTs) were generated (length=255 steps, consistency index (CI) = 0.3490, homoplasy index (HI) = 0.6510, Retention Index (RI) = 0.5840, Rescaled Consistency Index (RC) = 0.2038). All MPTs were nearly identical except for a few minor differences: under strict consensus the relative positionings of *Mictis tenebrosa* and *M. oceanensis* were unresolved, and in three of the trees the sister relationship of *Pseudomictis distinctus* and *P. obtusispinus* was not supported. One of the six trees where these relationships are resolved was chosen for all further discussion (Fig. 2.16). Despite low measures of overall support, several of the relationships presented are further reinforced by biogeography and are believed to reflect the true phylogeny, as discussed below.

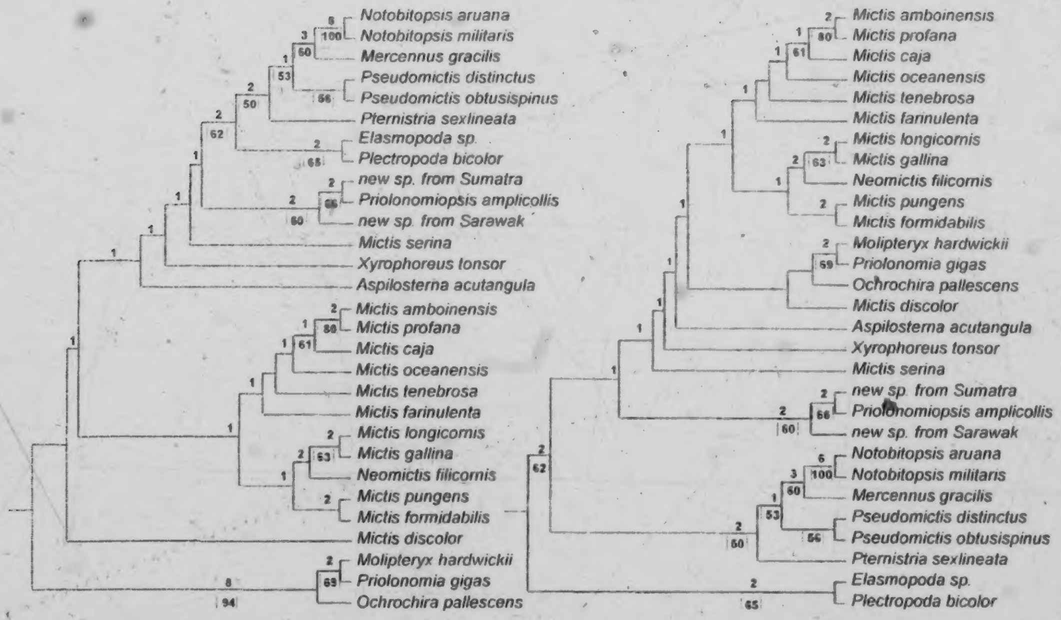
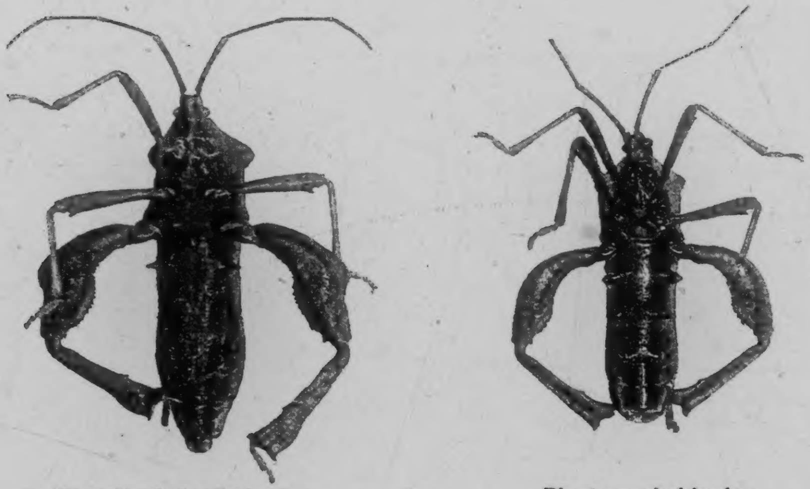

Notobitopsis aruana
Notobitopsis militaris
Mercennus gracilis
Pseudomictis distinctus
Pseudomictis obtusispinus
Pternistria sexlineata
Elasmopoda sp.
Plectropoda bicolor
new sp. from Sumatra
Priolonomiopsis amplicollis
new sp. from Sarawak
Mictis serina
Xyrophoreus tonsor
Aspilosterna acutangula
Mictis amboinensis
Mictis profana
Mictis caja
Mictis oceanensis
Mictis tenebrosa
Mictis farinulenta
Mictis longicornis
Mictis gallina
Neomictis filicornis
Mictis pungens
Mictis formidabilis
Mictis discolor
Molipteryx hardwickii
Priolonomia gigas
Ochrochira pallescens
Mictis amboinensis
Mictis profana
Mictis caja
Mictis oceanensis
Mictis tenebrosa
Mictis farinulenta
Mictis longicornis
Mictis gallina
Neomictis filicornis
Mictis pungens
Mictis formidabilis
Molipteryx hardwickii
Priolonomia gigas
Ochrochira pallescens
Mictis discolor
Aspilosterna acutangula
Xyrophoreus tonsor
Mictis serina
new sp. from Sumatra
Priolonomiopsis amplicollis
new sp. from Sarawak
Notobitopsis aruana
Notobitopsis militaris
Mercennus gracilis
Pseudomictis distinctus
Pseudomictis obtusispinus
Pternistria sexlineata
Elasmopoda sp.
Plectropoda bicolor

Figure 2.16. One of the 6 equally parsimonious phylogenetic reconstructions, A) rooted at the Derepteryx Group, and B) rooted at the Plectropoda Group. Length = 255 steps, CI = 0.3490, HI = 0.6510, RI = 0.5840, RC = 0.2038). Numbers above branches indicate Bremer support values, while boxed numbers below indicate Bootstrap support (n=100 reps). (Jackknife support values were virtually identical to Bootstrap values and are not shown).

The genus *Mictis* appears to divide into two groups that roughly conform to the following traits: those with small tibial spines, long terminal antennal segments, a white spot of setae on the metathorax and hind femora with a long stalk before the bend, and those will larger, more leaflike tibial spines, short terminal antennal segments, no white spot on the metathorax and femora with short stalks. Within the former, the sister relationship of *M. gallina* and *M. longicornis* is fairly well supported, and in the latter so is the relationship among *M. profana*, *M. amboinensis* and *M. caja*. In this reconstruction, the genus *Mictis* appears to be an artificial (i.e., non-monophyletic) unit, with *M. serina* and *M. discolor* separated from their congeners by several taxa. As well, *Neomictis filicornis* is now clustered within *Mictis*. If we choose to rearrange the tree, the cost in number of steps to return *M. discolor* to the rest of the genus is 2 additional steps, while the cost of returning *M. serina* back into the fold is 6 additional steps. Similarly the cost to drop *Neomictis filicornis* out of the genus is 5 steps.

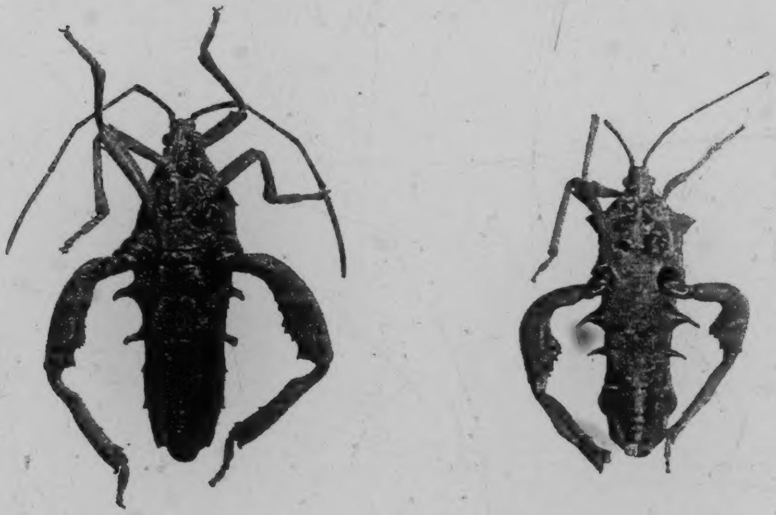
Relationships identified among taxa outside of *Mictis* show somewhat better support. Except for *Priolonomiopsis amplicollis*, the Derepteryx Group shows very strong support, as evidenced by high Bootstrap, Jackknife, and Bremer support values. Instead of clustering with the other Derepteryx Group species, *P. amplicollis* clusters with the two undescribed species from Indonesia.

There is also relatively strong support for the grouping of the two species of *Notobitopsis* from New Guinea, the two species of *Pseudomictis* from Vietnam and China, *Mercennus gracilis* from Borneo, Java and Singapore, and the genus *Pternistria*, of which all but one species are found exclusively in New Guinea (a single species is also found in Australia) with the two Plectropoda Group species from Africa. All of these species share a complex hindlimb morphology (Fig. 2.13), specifically with respect to tibial form. These characters alone could be a matter of convergence, however several of these species also share other unique structures: both species of *Pseudomictis* have rearward extensions of abdominal sternites III and IV, with a median tubercle on segment V as in *Plectropoda bicolor*, and *Mercennus gracilis* and *Pternistria sexlineata* both have paired median tubercles as in *Elasmopoda*. In addition, all species of *Pternistria* have lateral abdominal tubercles on segments III and IV, the character originally used by O'Shea to separate the Plectropoda and Mictis Groups (Fig. 2.17).



Pseudomictis distinctus

Plectropoda bicolor



Pternistria sexlineata

Elasmopoda sp.

1 cm

Figure 2.17. Structural similarities between Asian and African taxa are exemplified by the Asian species *Pternistria sexlineata* and *Pseudomictis distinctus,*and the African *Elasmopoda* sp. and *Plectropoda bicolor*. All four species have very similar hind femora and the same distinctive hind tibiae. *Pternistria* is the only Asian genus to possess 2 pairs of lateral abdominal tubercles, a condition typical of the African Plectropoda Group to which *Plectropoda* and *Elasmopoda* belong. Additionally, the Asian species *Pseudomictis distinctus* possesses a bifurcate median abdominal tubercle at the end of abdominal segment V, which is very similar to that of *Plectropoda bicolor.*

O'Shea's (1979) species groups and their relationships are not supported by the present analysis, since there is no means of rooting the tree that will recreate the relationships shown in Figure 2.1. Because of the strong relationship between the two African species and *Mercennus gracilis*, *Notobitopsis*, *Pseudomictis* and *Pternistria sexlineata*, I have chosen to root the tree with the Plectropoda Group rather than with the Derepteryx Group.

Several phylogenetic groupings are also supported by geographic distribution data. Notably, the species *M. profana*, *M. caja*, *M. amboinensis* and *M. oceanensis* all share a predominantly Australian and South Pacific distribution, *Molipteryx*, *Priolonomia gigas* and *Ochrochira pallescens* are all from mainland Asia through to India, and *Notobitopsis aruana*, *N. militaris* and *Pternistria sexlineata* are all from New Guinea (though the closely related genus *Pseudomictis* is found only in Southeast Asia and China, and *Mercennus gracilis* is found in Borneo, Java and Singapore). On the other hand, some apparently related species have very disparate distributions. For example, *Mictis pungens* and *M. formidabilis* are shown as sister species, yet the former has been found only in the Philippines while the latter is restricted to Sri Lanka.

Taxonomy

Revision of the Genus *Mictis*

Based on this phylogeny and with careful consideration of the characters used to generate it, I formally propose the removal of both *Mictis discolor* and *M. serina* from the genus *Mictis*. *Neomictis filicornis* is also retained as a separate (monobasic) genus outside of *Mictis*.

M. discolor differs from all other species of *Mictis* in several ways: a median tubercle is lacking (a condition admittedly shared by *M. gallina*, yet all other characters of. *M. gallina* place it well within *Mictis*), the hind femora have a dorsal serrated dilation, are not stalked at the base and are evenly curved throughout, the hind tibiae have a ventral spine different from that of all other species, the pronotal margins are completely smooth - a condition shared by *M. serina* - the distodorsal forked lobe of the aedeagus is strongly sclerotized, and paramere shape is different, with a prominent flattened inner lobe, again similar to that of *M. serina*.

M. serina also shows many characteristics which separate it from the genus: smooth pronotal margins, a uniquely shaped median abdominal tubercle flared out into lateral lobes, long, thin hind femora, tibiae much more like those of *Xyrophoreus tonsor* than *Mictis*, no lateral sclerotized lobes on the aedeagus, and a flattened inner lobe on the paramere.

Regarding *Neomictis filicornis*, several shared characters have resulted in a phylogenetic reconstruction which has placed this taxon within *Mictis*. This is not the first time this has occurred, as Blöte (1938) included it in *Mictis* under the name *M. tridentifer*. Lateral abdominal tubercles, a median abdominal tubercle on the margin of segments III and IV, paramere shape and several other characters all suggest some relationship, however closer inspection of these characters leads me to believe that the differences are of the generic rather than specific level. The pronotum shape is unique, hind femora are shaped much more like those of *Xyrophoreus* than *Mictis*, the median tubercle is extremely long and thin and the lateral tubercles are mounted on the tubercle itself, the genital capsule is extended posteriorly, the distodorsal lobe of the aedeagus is long and thin, and lateral sclerotized processes are absent. Because *M. tridentifer* is synonymous with *Neomictis filicornis*, **(new synonymy)** it must be removed from the genus *Mictis*.

After examining *M. amboinensis* from Ambon I cannot find sufficient differences to justify a separate species designation. I therefore propose that *M. amboinensis* be made a subspecies of *M. profana* **(comb. nov.)**. Likewise *M. macra* is said to differ from *M. gallina* only by its less incrassate hindlimbs (Distant 1902), which is insufficient grounds for separate species designations. I reassign this taxon to subspecies status, as *M. gallina macra* **(comb. nov.)**. Based on Hsiao's description and illustrations of *M. tuberosa* (1965), it is almost certainly identical to *M. longicornis*, and I formally declare it a junior synonym thereof **(new synonymy)**.

Although *M. dilatipes* is thought to be very similar to *M. profana* (O'Shea and Schaefer 1980), this similarity is not expressly described and without closer examination I refrain from synonymizing the two. Lastly, Hsiao's *M. angusta* (1965) is said to be most similar to *M. tenebrosa* but without a velvet white spot on the metathorax. Illustrations show a similar median abdominal tubercle, but the leaflike hind tibial spine is located further down the tibia than in *M. tenebrosa*. Without further information it is impossible to place this species with confidence. For the time being, I suggest *M. angusta* be retained at the species level in the genus *Mictis*.

Mictis Leach

Mictis Leach, 1815, Zoological Miscellany **1**: 92. Type-species: *Mictis crucifera*; monobasic.

> *Cerbus* Hahn, 1831, *Die Wanzeuartigen Insecten*, p.7. Type-species: *Cerbus fulvicornis* Hahn *nec* Fabricius; monobasic. Syn. by Stal, 1873.
>
> *Lygaeomictis* Blöte, 1938, *Zoölogische Mededeelingen*, **20**: 294. Syn. by O'Shea, 1980.
>
> Type-species: *Lygaeomictis mictus dilatipes* Blöte; monobasic.

(Taken from O'Shea and Schaefer 1980)

O'Shea and Schaefer (1980) revised the genera of Asian and Australian Mictini, including the genus *Mictis*. Their revision provides an excellent description of the genus, however their description of the male genitalia is inaccurate and does not reflect the true structure and variability expressed within this genus. Their genitalic description is based wholly on *M. profana*, thus ignoring the wide variability found throughout the genus.

Furthermore, based on their description and illustrations, they apparently relied on an incompletely inflated aedeagus to discuss structure, thereby incorrectly concluding that *Mictis* lacks paired distoventral lobes, which are in fact clearly visible in all species I have examined, including *Mictis profana*. Within *Mictis*, the aedeagus always has a bifurcate distolateral lobe, the tip of which is almost always at least slightly forked, paired distolateral lobes with weakly to strongly sclerotized lateral processes, and paired distoventral lobes. Paramere shape is also much more variable than is suggested by O'Shea and Schaefer (1980). In fact, paramere shape in *M. profana* is atypical for the genus, with almost all other species exhibiting parameres with long, curved and tapered tips. Of the species examined, only *M. amboinensis* and to a lesser extent *M. caja* have parameres akin to those of *M. profana*.

Key to the genus *Mictis*

For a key to the males of the Asian Mictini see O'Shea and Schaefer (1980). The following is a key to the genus *Mictis*, which is found throughout Asia, Australia and into the South Pacific. Because specimens of some taxa were unavailable for this study, they have been omitted from this key and their likely placement is discussed elsewhere.

1. White pubescent patch of setae on metathorax..2
   No white pubescent patch of setae on metathorax....................................6
2. Tibial spine large and leaflike, half-way down tibia...............................3
   Tibial spine small, around 2/3 down tibia...4
3. Humeral angles extended almost as wide as head into serrate points, prominent median abdominal tubercle, lateral tubercles lacking (Sri Lanka).. ....*Mictis formidabilis* Distant 1918

Humeral angles rounded, not extended as wide as head, median and lateral abdominal tubercles present (India, Burma, China, Vietnam, Malaysia, Indonesia)………………………………………………………………………*Mictis tenebrosa* (Fabr. 1717)

4. Median and lateral abdominal tubercles present……………………………………5

No median abdominal tubercle, only lateral tubercles present (India, Burma…)………………………………………………………………………*Mictis gallina* Dallas 1852

5. Humeral angles only slightly extended, median abdominal tubercle large, recurved and thumblike in larger specimens, hind femora serrate along ventral margin (Malay Peninsula, Java, Borneo, Philippines)……….. *Mictis longicornis* Westwood 1842

Humeral angles extended as wide as head, median abdominal tubercle not thumblike in larger specimens (Philippines)…………………………*Mictis pungens* Stal 1870

6. Humeral angles extended outwards and sharply angled upwards, margins serrate (Lombok, Philippines)……………………………………….*Mictis farinulenta* Breddin 1899

Humeral angles variable but not sharply angled upwards, margins variable……..7

7. Caudal margin of metathorax cream coloured, humeral angles subacute, margins serrate (New Hebrides)……………………………………………………*Mictis caja* Stal 1865

Caudal margin of metathorax not pale, humeral angles somewhat pointed……..8

8. Yellow cross on hemelytra, pronotum moderately tuberculate (Java, Sulawesi, Lesser Sunda Islands, New Guinea, Australia, Fiji, New Caledonia, Solomon Islands)……………………………………………………………*Mictis profana* (Fabr. 1803)

No yellow cross on hemelytra, pronotum strongly tuberculate (New Hebrides)……………………………………………………………………*Mictis oceanensis* Distant 1900

Diagnoses of *Mictis* species

Mictis profana (Fabricius, 1803); Indonesia, New Guinea, Australia, British Solomon Islands, New Caledonia, Fiji, Samoa.

Included subspecies:

amboinensis (Walker, 1871); Ambon, Buru Island. comb. nov. for *M. amboinensis* Walker.

Bright yellow cross on hemelytra is diagnostic. Tibial spine large and leaflike, median abdominal tubercle large and weakly cleft, but may be almost absent in smaller individuals. Lateral spines are blunt and dorsoventrally compressed. Paramere body is long and narrow, while the paramere tip is short and angular.

M. profana amboinensis differs from *M. profana* in that the yellow cross on the hemelytra is much more faint, and body size is generally slightly greater.

M. caja Stal, 1865; Queensland.

Pale cream colouring on the caudal margin of the metathorax is diagnostic. Superficially very similar to *M. profana* and *M. profana amboinensis*, but lacking a yellow cross on the dorsum. Additionally, when the wings are opened the dorsal surface of the abdomen is banded yellow and black in *M. caja*, not solid red or orange. Aedeagus with large, plate-like lateral sclerotized processes. Paramere is relatively simple with short curved arm, lacking any substantial texturing on inner surface of concavity. Tibial spine large and leaflike, median abdominal tubercle large and weakly cleft. Lateral spines are blunt and dorsoventrally compressed.

M. farinulenta Breddin, 1899; Lombok, Philippines.

Humeral angles sharply angled upwards distinguish this species from all others. Paramere with very thin scythe-like arm, outer margin humped, large knob at base of arm on inner concavity. Tibial spine is large and leaf-like, lateral abdominal tubercles are small and median tubercle is simple.

M. formidabilis Distant 1918; Sri Lanka.

Pale cream coloured patch of setae on the metathorax above the hind coxa unites *M. formidabilis* with *M. longicornis*, *M. gallina*, and *M. pungens*. *M. formidabilis* has substantially extended humeral angles as in *M. pungens*, however unlike *M. pungens M. formidabilis* has a leaf-like hind tibial spine and lacks lateral abdominal tubercles.

M. gallina Dallas, 1852; India, Burma, Laos.

Included subspecies:

macra (Stal, 1865); Assam. comb. nov. for *Mictis macra* Stal.

White patch of setae on the metathorax above the hind coxa. Very similar to *M. longicornis*, except *M. gallina* lacks a median abdominal tubercle. As well, the dorsal surface of the abdomen is dark with two pale yellow spots, a condition found only in one other species, *M. tenebrosa* (Fig. 2.14). Hind tibial spines are relatively small, 2/3 down the tibia as in *M. longicornis*, and *M. pungens*. Distolateral lobes of aedeagus project outward, lateral sclerotized process present. Paramere strongly curved, outer margin arched, inner concavity wrinkled and with a prominent rectangular tubercle.

M. gallina macra from Assam is nearly identical but with posterior legs more slender, less thickened and less dentate.

M. longicornis Westwood, 1842; Malaysia, Java, Borneo, Philippines, China.

White patch of setae on the metathorax above the hind coxa. Superficially similar to *M. gallina*, but large specimens of *M. longicornis* have a large, recurved median abdominal tubercle reminiscent of a thumb. Smaller individuals have much smaller median abdominal tubercles which may go unnoticed, but dorsal surface of abdomen is bright orange unlike in *M. gallina*. In addition to the patch of setae on the metathorax, some specimens from West Java also have a faint cream coloured strip of setae on the pro- and mesothorax. Genitalia are nearly identical to that of *M. gallina*.

M. pungens Stal, 1870; Philippines

White patch of setae on the metathorax above the hind coxa. Extension of humeral angles as far as width of head distinguishes *M. pungens* from other species with patch of setae on the metathorax. Median abdominal tubercle very similar to that of *M. longicornis* but less recurved. Hind tibia narrowly dilated down to spine, 2/3 down tibia. Lateral lobes of aedeagus similar to those of *M. longicornis* and *M. gallina*, but lateral processes only weakly sclerotized. Paramere as in *M. longicornis* and *M. gallina* but without prominent tubercle on inner concavity.

M. tenebrosa (Fabricius, 1787); India, Burma, China, Vietnam, Malaysia, Indonesia.

Subacute humeral angles and smooth lateral margins help to distinguish *M. tenebrosa* from those other species of *Mictis* that possess a white patch of setae on the metathorax. The dorsal surface of the abdomen is dark metallic blue (dark brown in death) with pale lateral spots near the base as in *M. gallina*, however unlike *M. gallina*, *M. tenebrosa* has a prominent median abdominal tubercle and the tibial spine is leaf-like and situated half-way down the tibia.

Two New Species of *Priolonomiopsis* O'Shea 1980.

In the phylogenetic analysis above both new species described here group with *Priolonomiopsis amplicollis*. Superficially the new species from Sumatra is most similar, as it shares identical pronotal and hind tibial structure with *P. amplicollis*, as well as overall body shape and general paramere shape. As in *P. amplicollis* the distodorsal lobe of the aedeagus is not forked, however unlike *P. amplicollis* the distolateral lobes are weakly sclerotized along their dorsal margins. Additionally, *P. amplicollis* possesses two median abdominal tubercles, one small one on the margin of segments III and IV and another much larger one on the margin of segments IV and V, whereas the specimen from Sumatra has only a single tubercle on III and IV. However, the wide variability in abdominal tubercle location and form throughout the taxa under study leads me to believe that the underlying genetic mechanisms for tubercle placement might involve very little genetic change. With this in mind, I formally designate this as *Priolonomiopsis sumatra* **(new species)**.

As for the specimen from Sarawak, it's relationship with *Priolonomiopsis* is less certain. Unlike *P. amplicollis*, it has narrowly pointed humeral angles, different tibial and femoral structure, a single median abdominal tubercle on segments III and IV, and lateral spines on III. The presence of lateral abdominal tubercles is of little concern, since *P. spinifera* also has small lateral tubercles. As in *P. amplicollis*, the distodorsal aedeagal lobe of the species from Sarawak is not forked, nor does it have lateral sclerotized processes. Although I regard the evidence of relationships as somewhat weak at present, I describe the species as *Priolonomiopsis sarawensis* (**new species**) in this review.

Priolonomiopsis sumatra; Sumatra. new species

Type. – Holotype male: Indonesia, Sumatra, Aceh, Gunung Leuser National Park, Ketambe Research Station, October 1999, D.C. Darling. Collected by Malaise trap in primary rainforest, closed canopy, 350 m. 3^0 41' N, 97^0 39' E. Deposited at the Royal Ontario Museum, Toronto.

– Female unknown.

Description. – Male (holotype). Dorsal colouration: Head and pronotum dark mauve with gold pubescence; antennal segments I-III cherry red, segment IV slightly paler; scutellum slightly darker than pronotum with yellow apex; clavus and corium dark mauve as pronotum, inner margin bordering scutellum orange; hemelytral membrane dark brown to black; abdominal tergites orange, connexival segments dark mauve with yellow marks at each apical margin. Ventral colouration: dark mauve with pale pubescence; trochanters slightly darker with some yellow-orange patterning; dorsal margin of fore and middle tibiae yellow; tarsi fringed with orange pubescence. *Structure.* – Head: Rostrum almost reaches middle coxae; antennifers separated; antennae long and thin, segment IV almost as long as I, curved. Thorax. Pronotum: steep; collar narrow, frontal margins not projecting forward; lateral margins jagged; dorsal surface nodulose; humeral angles broadly pointed, projecting laterally and slightly upwards; posterior margin straight. Metathoracic scent gland: situated relatively basolaterally, immediately before middle coxae; anterior auricle extended up and forward; posterior auricle small and round. Legs: fore and middle femora cylindrical, slightly expanded distally, 2 distinct subapical spines on ventral surface; fore and middle tibiae slender and sulcate, expanding slightly to apex; hind trochanter with small spine; hind femora incrassate, sharply curved near base, reaching back to beginning of abdominal segment VII; ventral margin slightly expanded immediately after curve with finely serrated ridge ending in two subapical spines; hind tibiae shorter than femora, straight, laterally compressed with prominent dorsal and ventral dilations; dorsal dilation rounded and tapering down to apex, ending in a small subacute spine; ventral dilation with prominent spine 1/3 from base then tapering sharply to apex. Scutellum: Triangular, laterally striated. Hemelytra: Macropterous, reaching apex of last abdominal segment. Abdomen: Weakly expanding until end of segment V then narrowing to genital capsule, connexival segments slightly sulcate, lateral margins weakly nodulose; Ventral margin of abdominal segments III/IV projecting into a median abdominal tubercle, middle of tubercle extended back into segment IV; anterior surface of median tubercle weakly laterally striated; segment III not armed with lateral spines or tubercles; in profile abdomen concave post-tubercle (Fig. 2.18). Genital capsule: Post-dorsal margin weakly projected posteriorly; lip of capsule upturned medially, downturned at sides, with shallow vertical groove in centre. Paramere (Fig. 2.3x): Tip long, curved and cylindrical, back of body humped, inner surface bulged, body dark brown, tip orange. Aedeagus (Fig. 2.6d):

Distodorsal lobe tapered, apex not forked or cleft, paired ventral lobes prominent, lateral lobes weakly sclerotized along dorsal margin.

Measurements. – Holotype male. Head length: 2.04 mm; width across eyes: 2.64 mm; interocular space: 1.44 mm; interocellar space: 0.84 mm; antennal segment lengths: I, 6.98 mm; II, 5.53 mm; III, 4.58 mm; IV, 6.60 mm. Pronotal length: 6.62 mm; width across collar: 2.17 mm; width across humeral angles: 10.75 mm; Scutellar length: 3.25 mm; width: 3.17 mm. Fore femur length: 7.33 mm. Fore tibia length: 6.33 mm. Middle femur length: 7.58 mm. Middle tibia length: 7.50 mm; Hind femur length: 11.08 mm. Hind tibia length: 10.40 mm; width at ventral spine: 4.07 mm. Maximum abdominal width: 7.67 mm. Body length: 25.70 mm.

(Habitus: Fig. 2.18)

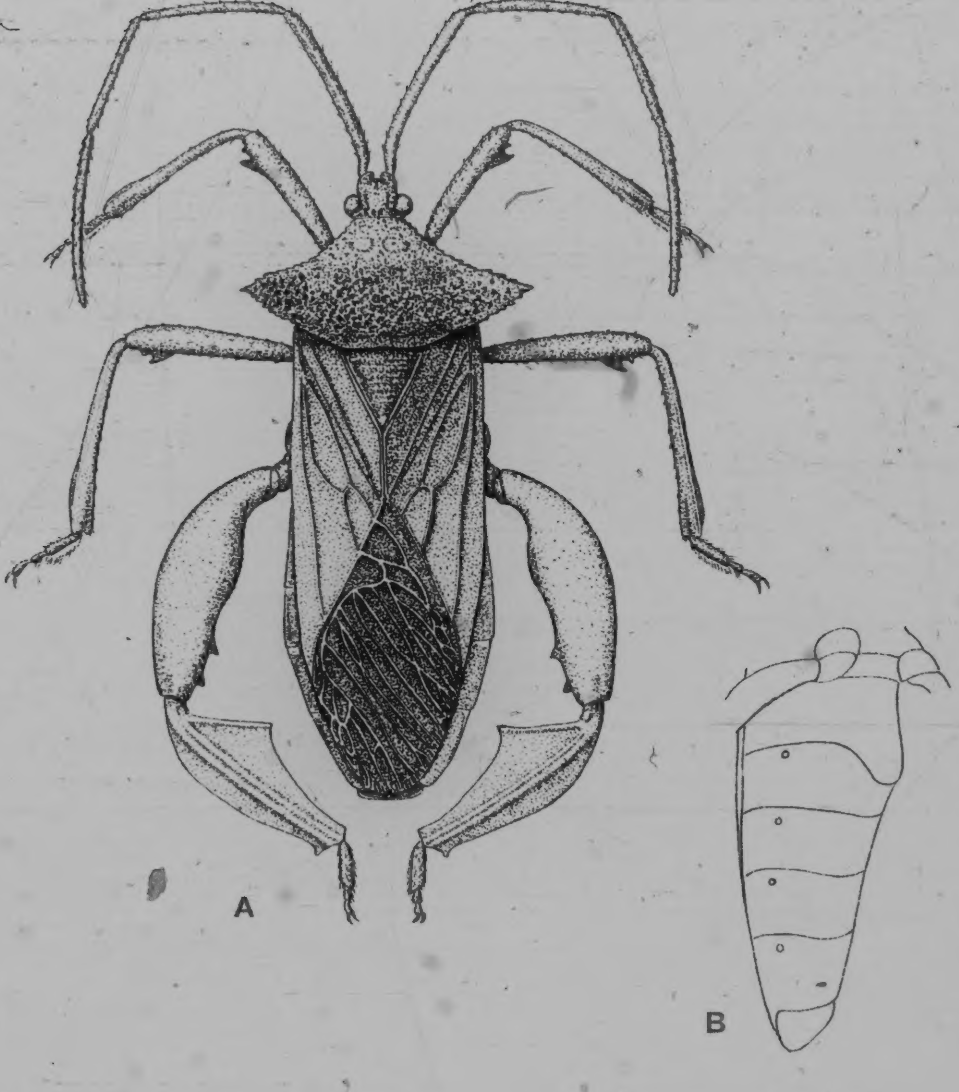


Figure 2.18. *Priolonomiopsis sumatra*. Holotype male. A) Dorsal view, and B) ventrolateral view of abdomen.

Priolonomiopsis sarawensis; Sarawak. new species

Types. – Holotype male: Malaysia, Sarawak, Sarikei District, Rejang Delta, July 15-26 1958, T. C. Maa. Deposited at the Bishop's Museum, Hawaii.

– Female unknown.

Description. – Male (holotype). Dorsal colouration: Head, antennae, pronotum and hindlimbs reddish brown with pale pubescence; scutellum reddish brown with yellow apex; clavus and corium reddish brown as above; hemelytral membrane dark brown to black; abdominal tergites pale yellow-orange, connexival segments reddish brown with yellow marks at each apical margin. Ventral colouration: yellowish brown with pale pubescence; trochanters slightly darker with some yellow-orange patterning; fore and midlimbs yellowish brown. Metathoracic scent gland: anterior auricle yellow.

Structure. – Head: Rostrum almost reaches middle coxae; antennifers separated; antennae long and gracile, (segment IV missing on specimen). Thorax. Pronotum: steep; collar narrow and punctate, frontal margins not projecting forward; lateral margins more or less smooth, becoming serrate at humeral angles; dorsal surface unevenly honeycombed; humeral angles pointed, projecting laterally and slightly upwards; posterior margin straight, angled down. Metathoracic scent gland: situated relatively basolaterally, immediately before middle coxae; anterior auricle rounded and concave; posterior auricle small and narrow. Legs: fore and middle femora cylindrical, slightly expanded distally, 2 distinct subapical spines on ventral surface; fore and middle tibiae slender and sulcate, expanding slightly to apex; hind femora incrassate, weakly curved, reaching back to beginning of abdominal segment VII; ventral margin with finely nodulose ridge near apex, with one finlike, acute subapical spine; hind tibiae shorter than hind femora, straight, laterally compressed; dorsal margin with a very narrow, straight dilation running the entire length, ending in a small, blunted spine; ventral margin with one subapical spine near apex, narrowly dilated then ending in smaller apical spine. Scutellum: Triangular, laterally striated. Hemelytra: Macropterous, reaching apex of last abdominal segment. Abdomen: Narrow but weakly expanding until end of segment V then narrowing to genital capsule, connexival segments more or less flat, lateral margins smooth; Ventral margin of abdominal segments III/IV projecting into a median abdominal tubercle, middle of tubercle extended back into segment IV, weakly grooved in the middle; anterior surface of median tubercle weakly laterally striated; segment III armed with small lateral spines. Genital capsule: Not projected posteriorly or dorsally; lip of capsule damaged on specimen. Paramere (Fig. 2.3y): Tip long, gently curved and cylindrical, outer margin straight, inner surface bulged. Aedeagus (Fig. 2.6c): Distodorsal lobe tapered, apex not forked or cleft, paired ventral lobes prominent, lateral lobes without sclerotized processes.

Measurements. – Holotype male. Head length: 1.80 mm; width across eyes: 2.80 mm; interocular space: 1.40 mm; interocellar space: 0.80 mm; antennal segment lengths: I, 5.89 mm; II, 4.70 mm; III, 3.62 mm; IV, missing. Pronotal length: 5.20 mm; width across collar: 2.20 mm; width across humeral angles: 11.52 mm; Scutellar length: 2.92 mm; width: 2.92 mm. Fore femur length: 6.50 mm. Fore tibia length: 5.83 mm. Middle femur length: 6.67 mm. Middle tibia length: 5.91 mm; Hind femur length: 10.25 mm.

Hind tibia length: 9.17 mm; width at ventral spine: 1.33 mm. Maximum abdominal width: 6.41 mm. Body length: 24.08 mm.

(Habitus: Fig. 2.19)

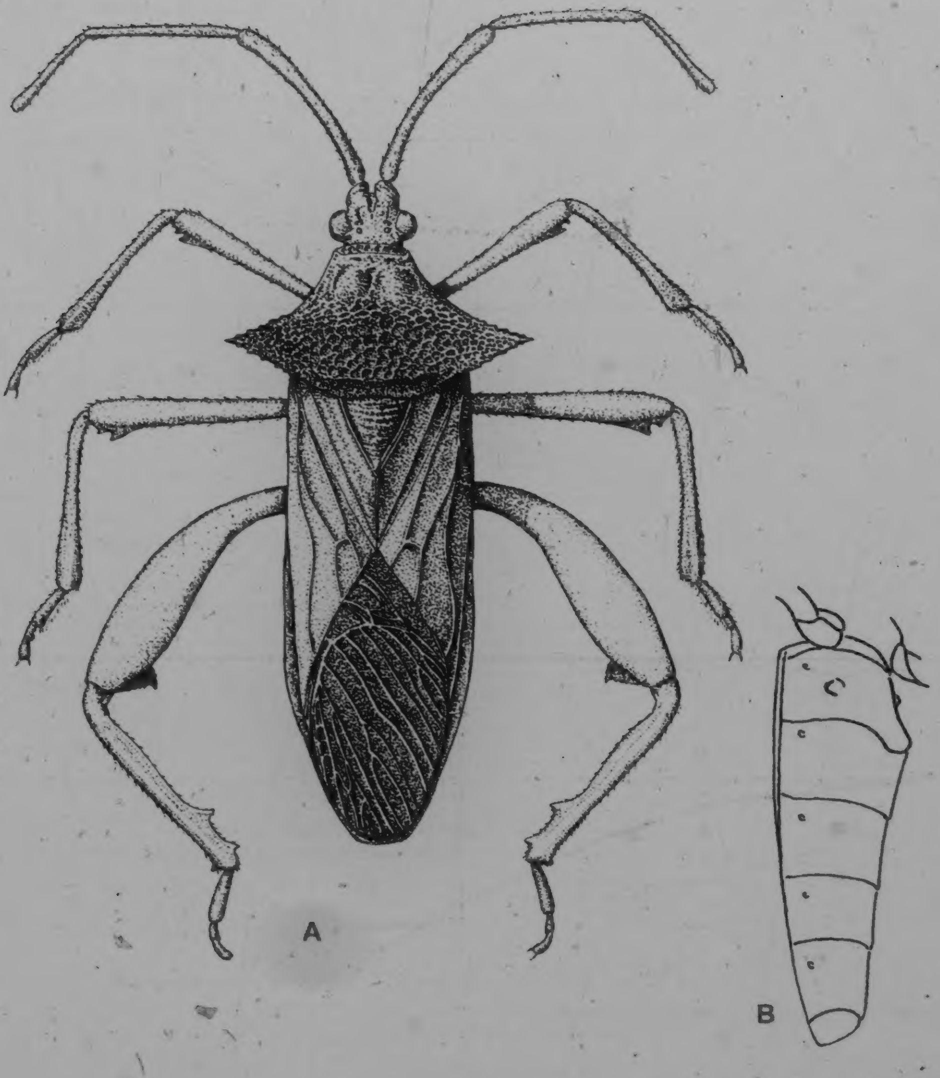


Figure 2.19. *Priolonomiopsis sarawensis*. Holotype male. A) Dorsal habitus (terminal antennal segments missing) and B) ventrolateral view of abdomen.

Conclusions

The Asian Mictini appear to be a very old group of organisms living in an even older, geographically complex region. Given their isolated ranges and the geographic history of the region, many included species have likely been isolated from one another for extremely long periods of time. The result is a that all species are readily identifiable by numerous unique attributes, and yet many are also confoundingly difficult to fit into a genealogical tree, in part because of these unique traits. There is no suite of characters showing gradual change from one taxon to the next, linking them together into a cohesive, ordered phylogeny. Instead, we have a number of different characters all telling a very different story, or no story at all. Furthermore, many of the most distinguishing characters are likely under sexual selection, thereby introducing as much opportunity for convergence as for divergence.

Occasionally several complex characters are retained after speciation and provide compelling evidence of common ancestry, as in the various abdominal and hindlimb characters that unite *Plectropoda bicolor* and *Elasmopoda* sp. with a small group of Asian taxa. At the same time we have a group of organisms like the genus *Mictis*, who are all more or less quite similar in appearance, yet have very few features that vary consistently enough to clearly establish either their relationships to one another or, equally importantly, their relationships to other genera. It is within this framework that taxonomists must choose which organisms are worthy of generic rank, and how these genera should be organised.

The Mictini are an old group (high levels of homoplasy and their distribution throughout the Old World tropics suggest so), whose origin likely lies in Africa. Even though O'Shea's (1979) relationships among species groups are probably incorrect, it is still quite possible that there have been several colonisation events of Asia from Africa, as his reconstruction implied.

Let us consider those species shown here to be most closely related to the two African species. The uncanny similarity between *Pternistria sexlineata* and *Elasmopoda* convinces me that these two are somehow closely related. Likewise the genus *Pseudomictis* looks to share a common ancestry with *Plectropoda bicolor*. In my reconstruction all of these taxa group together, along with *Notobitopsis* and *Mercennus gracilis*. When we examine their geographic distributions, we see that the genus *Pternistria* is restricted to New Guinea (except for one species in Australia), and *Pseudomictis* is restricted to Southeast Asia and China. This could reflect east-west dispersal (or west-east), but it might also be evidence of separate colonisation events from a pool of common ancestors. Perhaps the ancestors of *Pternistria* had a Gondwanaland distribution (this is the only time the African and New Guinean land masses were ever in close proximity), and were brought to Southeast Asia on New Guinea some 20 million years ago (Hall 1995, 1997). At the same time, the ancestors of *Pseudomictis* may have entered Asia over land from the west, or maybe they rafted over on India, which broke off from Gondwanaland around 120 Ma. and collided with Asia about 15-20 mya (Turner *et al.* 2001). As we add more and more taxa to the puzzle, sorting out relationships and points of origin becomes ever more complex.

Since the Asian Mictini are probably born out of multiple colonisation events by multiple lineages, a clear picture of their phylogenetic and biogeographic history can only be achieved with full consideration of both the Asian and African faunas and, unfortunately, this lies beyond the scope of the present work.

This phylogenetic analysis is the first to test our current understanding of species group relationships within the Mictini s.s. using both Asian and African species. The results have shown us that our current assumptions do not hold true, and that unravelling these relationships will probably require a careful consideration of the tribe's biogeographic history. Along with a thorough consideration of each character, this analysis was also used to revise the genus *Mictis* and to name two undescribed species of *Priolonomiopsis*. This study has shown that a cladistic approach can be very useful in determining the evolutionary history of the Mictine coreids, as well as for revising the current taxonomy and the placement of new species.

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Chapter 3

Scaling Relationships and Sexual Dimorphism in *Mictis profana*

Introduction

Scaling relationships of various body structures with body size can provide evidence of the selection pressures which help to mould those structures and associated behaviours. In isometric relationships, similar proportions are maintained across all body sizes. However, it is common for some organisms in a population to express disproportionately larger (or smaller) structures than others in relation to their body size. Furthermore, it is often only one sex within a species – generally the male – that expresses such disproportionate traits, a phenomenon known as sexual dimorphism.

Darwin (1871) was the first to suggest that these sexually dimorphic characters might confer some advantage to the reproductive success of their possessors, and so evolve under sexual selection. These dimorphic characters are generally thought to show allometric growth patterns, whereby larger males display significantly larger structures than smaller males. This pattern is reflected in slopes significantly greater than 1.0 in log-log regressions for males of the given structure on some indicator of body size, such as body length or pronotal width (Eberhard 1998), with females showing smaller slopes.

Emlen (1997) and Emlen and Nijhout (2000) however, warn us that these allometric relationships are not absolute, but are themselves dependant on how a particular organism's genotype responds to extraneous factors, such as environmental conditions and population structure. In other words, the realized structure of an individual actually represents only one point in a continuum of that genotype's phenotypic potential. Emlen and Nijout (2000) also urge caution in the quest for allometric relationships, as some traits do not necessarily conform to a linear scaling relationship, and may instead be sigmoid, discontinuous or curved. It is important then, when studying scaling relationships, to take into consideration the environmental conditions underlying all individuals under study and to look at the non-transformed scaling data to determine what model best describes the relationship.

Scaling relationships in Coreidae

Many leaf-footed bugs (Heteroptera: Coreidae) have enlarged and armed hindlimbs. Mitchell (1980) was the first to show that the enlarged hindlimbs of the coreid *Acanthocephala femorata* function in male-male combat. Eberhard (1998) later revealed that in males of *A. declivis* these hindlimbs are allometrically-scaled to overall body size, suggesting that they are under strong sexual selection pressures. Miyatake (1997) further explored the functional morphology of male hindlimbs in *Leptoglossus australis*, discovering that of all hindlimb measures, femur length and width appeared to be under the strongest sexual selection and were functionally significant in male-male combat. Interestingly, hind tibial characters – which are also sexually dimorphic – did not show allometric scaling in his study.

There are many other aspects of coreid structure which also exhibit sexual dimorphism, but have not been looked at in terms of their scaling relationships or functional significance. In particular, within the coreid tribes Mictini, Acanthocorini and

Petascelidini (O'Schea and Schaefer 1978), males of many species possess prominent ventral abdominal tubercles, the purpose of which is entirely unknown.

This chapter explores the scaling relationships of various morphological characteristics of the leaf-footed bug *Mictis profana* (Heteroptera: Coreidae), and relates these to selection pressures and environmental conditions. Through measures taken from wild-caught individuals as well as their laboratory-reared offspring, this study shows that male secondary sexual characteristics, particularly median abdominal tubercles in *M. profana*, exhibit a high degree of allometric scaling.

Materials and methods

Organisms

Found only in the Old World, members of the tribe Mictini *s.s.* feed mostly on the fruits and young shoots of legumes (Schaefer and O'Shea 1979, Schaefer and Mitchell 1983). While most members of the tribe are restricted to Southeast Asia, the Crusader bug, *Mictis profana*, is also found in Australia and throughout the South Pacific. As with other mictine coreids, *M. profana* is highly sexually dimorphic, with males possessing curved and incrassate hind femora, ventrally armed hind tibiae and prominent ventral and ventrolateral abdominal tubercles, while females, as is typical of the tribe, express the essentially unmodified version of these traits. This dimorphism between male and female leg structure is readily apparent as early as the 3rd instar, whereas male abdominal tubercles do not manifest themselves until the final moult into the adult (personal observation).

Data collection and analyses

Insects were collected from an experimental pigeon pea (*Cajanus cajan*) plot at the Koronivia Field Station, Viti Levu, Fiji between January 1st and March 11th, 2001. Approximately 30 live individuals were brought back to Canada (Canadian Food Inspection Agency Permit no. P-2002-01758) and a colony established at the University of Alberta. This colony was maintained on a diet of live pigeon pea plants, snow pea pods and peeled orange slices. Significant efforts were made to maintain a constant growth environment (~25^{0}C, 60-80% relative humidity), however lack of fresh produce coupled with extremely cold temperatures and desert-like low ambient humidity in the winter sometimes made this impossible. Measurements were taken from 34 adult males and 25 females: this sample included both wild-caught insects (N_{males} = 12, $N_{females}$ = 8) as well as their laboratory-reared progeny. Measurements included overall body length, maximum pronotal width, mid-femur length and maximum depth (left leg) hind femur length and maximum depth (left leg), hind tibial length and maximum depth (left leg; in males this was across the tibial spine, in females across the corresponding ventral tibial dilation and tubercle length (Fig. 3.1). In males this was taken from the point where the border of segments III and IV is distinctly angled to the rear, and measured out from here to the apex of the tubercle. Though females lack a distinct tubercle they also show a rearward deflection of the margin of segments III and IV, so female tubercle depth was measured from that point to the apex of the abdomen. All body measurements were made with Vernier calipers except for abdominal tubercle depth, which was measured using a calibrated ocular micrometer at 20X magnification. Voucher specimens have been placed in the collections of the Strickland Entomological Museum, Edmonton Alberta, and the Royal Ontario Museum, Toronto Ontario.

A modification of the Student's t-test, which controls for the possibility of unequal variances, was used to test for dimorphism in mean trait values between the sexes (Bailey 1997). Relative amounts of variation in each measure were calculated, and are reported here as coefficients of variation (CV). Analysis of variance was employed to test for differences in variance between male and female measures.

Scaling relationships of the various body parts on body length were compared in several ways. Allometry of traits with respect to body length was assessed using reduced major axis (RMA) log-log regressions (Sokal and Rohlf 1995): the Student's t-test was used to test for significance of slopes. ANCOVA was used to test for sex effects on scaling relationships between the sexes. To maximize the ability of ANCOVA to detect differences in intercept, all variables were standardized by rescaling on the mean. The Student's t-test was then used to look for significant differences in RMA slopes between the sexes (for heteroscedastic data pairings the t-test was modified accordingly, as described in Bailey 1997).

Most studies of scaling relationships typically use collections of individuals exclusively sampled from either the wild or from museum collections, and so the possible effects of the environment on growth patterns are lost (Emlen and Nijhout 2000). In contrast, data presented here include measures from both wild-caught insects as well as their laboratory-reared young. To ensure that scaling relationships were consistent between these two groups, datasets were compared between wild and laboratory-reared males.

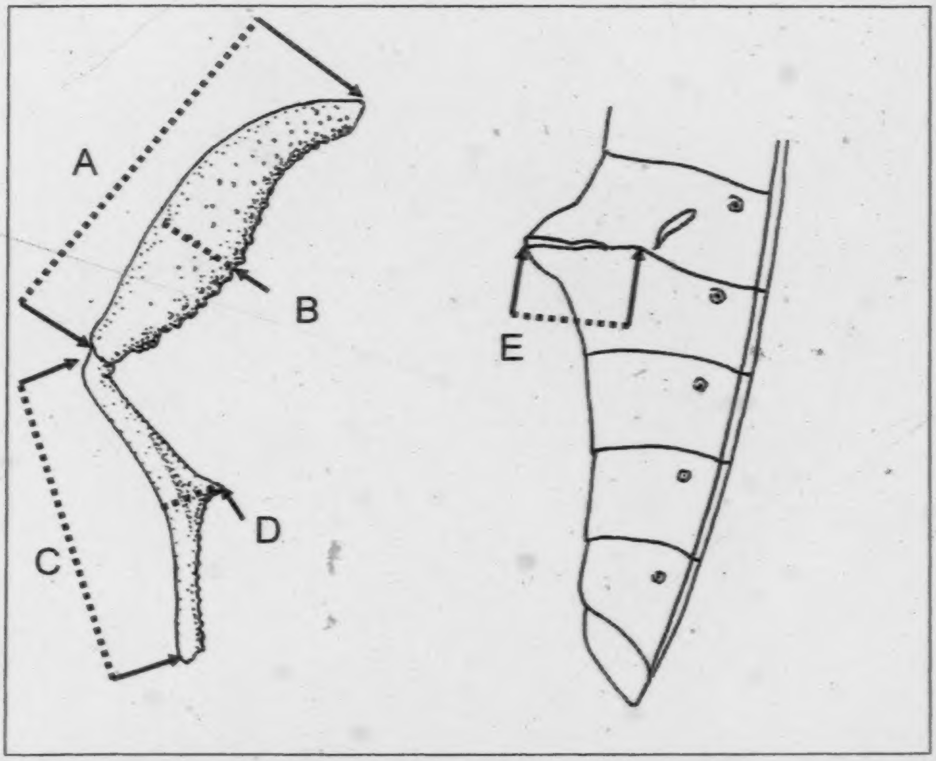

Figure 3.1. Measures of male hind femur length (A), maximum hind femur depth (B), hind tibial length (C) maximum hind tibial depth (D) and median tubercle depth (E). Though females lack a distinct tibial spine and median tubercle, measures were taken from the same landmarks.

Results

Sexual dimorphism in mean values

Male and female *M. profana* did not differ significantly in mean body length, although several other measures did exhibit marked size dimorphism. The greatest dimorphism was seen in median tubercle depth, with measures for males being 63.1% larger than those of females. This is not surprising, since females do not in fact possess a median abdominal tubercle, and the female measures really only reflect abdominal depth from the landmark used to the centre of the abdomen. Tibial depth was much deeper for males than females (41.5% dimorphism); again this is not unexpected, since only males possess a ventral tibial spine, whereas female tibiae are essentially unarmed. In terms of hind femoral measures, depth was almost 20% greater in males, whereas hind femoral length was not dimorphic. In some measures females were significantly larger, namely in pronotal width (10.1% dimorphism), and to a lesser extent hind tibial length (5.5% dimorphism) (Table 3.1).

When tested for equality of variance, hind femur depth, hind tibial depth and median tubercle depth were all found to be heteroscedastic ($p<0.05$), with males showing substantially more variation. This relatively higher variability in males is reflected in higher coefficients of variation (CV) in these traits (Table 3.1).

Table 3.1. Means, standard deviations (SD) and coefficients of variation (CV) of various body measurements for *M. profana* males and females, with t-test results testing for significant differences between the sexes (*ns* indicates non-significant *p*-values).

	Males (n=34)			Females (n=25)					
Measure	Mean (mm)	SD (mm)	CV (%)	Mean (mm)	SD (mm)	CV (%)	t	*p*	Dimorphism (% difference)
Body length	21.23	1.96	9.2	21.81	1.67	7.7	1.644	*ns*	2.7
Midfemur length	6.75	0.58	8.6	6.77	0.56	8.3	0.101	*ns*	0.3
Midfemur depth	1.02	0.14	13.7	1.07	0.10	9.3	0.555	*ns*	4.7
Pronotal width	7.16	0.67	9.4	7.96	0.77	9.7	3.560	<0.001	10.1
Hind femur length	9.35	1.11	11.9	9.64	0.95	9.9	1.091	*ns*	3
Hind femur depth	2.23	0.44	19.7	1.81	0.24	13.3	2.797	<0.05	18.8
Hind tibial length	8.91	0.75	6.4	9.43	0.86	9.1	2.488	<0.05	5.5
Hind tibial depth	1.88	0.29	15.4	1.10	0.15	13.6	6.471	<0.001	41.5
Median tubercle depth	0.84	0.36	42.9	0.31	0.09	29.0	4.450	<0.001	63.1

Scaling relationships

All nontransformed body measurements tested were positively correlated with overall body length, and none appeared to diverge from linearity (Fig. 3.2). Some degree of allometric scaling against body length was exhibited for many measures in both males and in females: only male hind tibial length and male pronotal width were isometrically scaled with body length. Male abdominal tubercle length had by far the highest allometric value (RMA slope = 6.017), followed by male hind femur depth (2.196) (Table 3.2).

ANCOVA results showed that scaling relationships differed significantly between sexes for pronotal width, hind tibial length and depth, hind femoral depth and median tubercle depth. For all but tubercle depth these differences were explained by intersexual differences in interecept of the least-squares regression of the trait on body length.

However, only for the relationship of tubercle depth and body length did the slopes differ significantly between the sexes (Student's t tests, Table 3.2).

Wild vs. lab-reared individuals

On average, insects reared in the laboratory were significantly smaller than those caught in the wild, $\bar{x}_{wild} = 22.70$ mm, $\bar{x}_{lab} = 20.43$; $t = 4.62$, $p<0.001$), with most of the measures from the wild-caught individuals (smaller sample size) falling within the upper range of the lab-reared insects. Body length, hind femur depth and tubercle depth were all found to be heteroscedastic. When log-log linear regressions were compared, all but one slope were found to be parallel. Only pronotal width showed a significant difference, with the slope for wild caught-males being higher than that for the lab individuals. Unfortunately, because of a fairly small sample size most r^2 values for the wild-caught individuals were exceedingly low, thus these results should be taken with caution (Table 3.3).

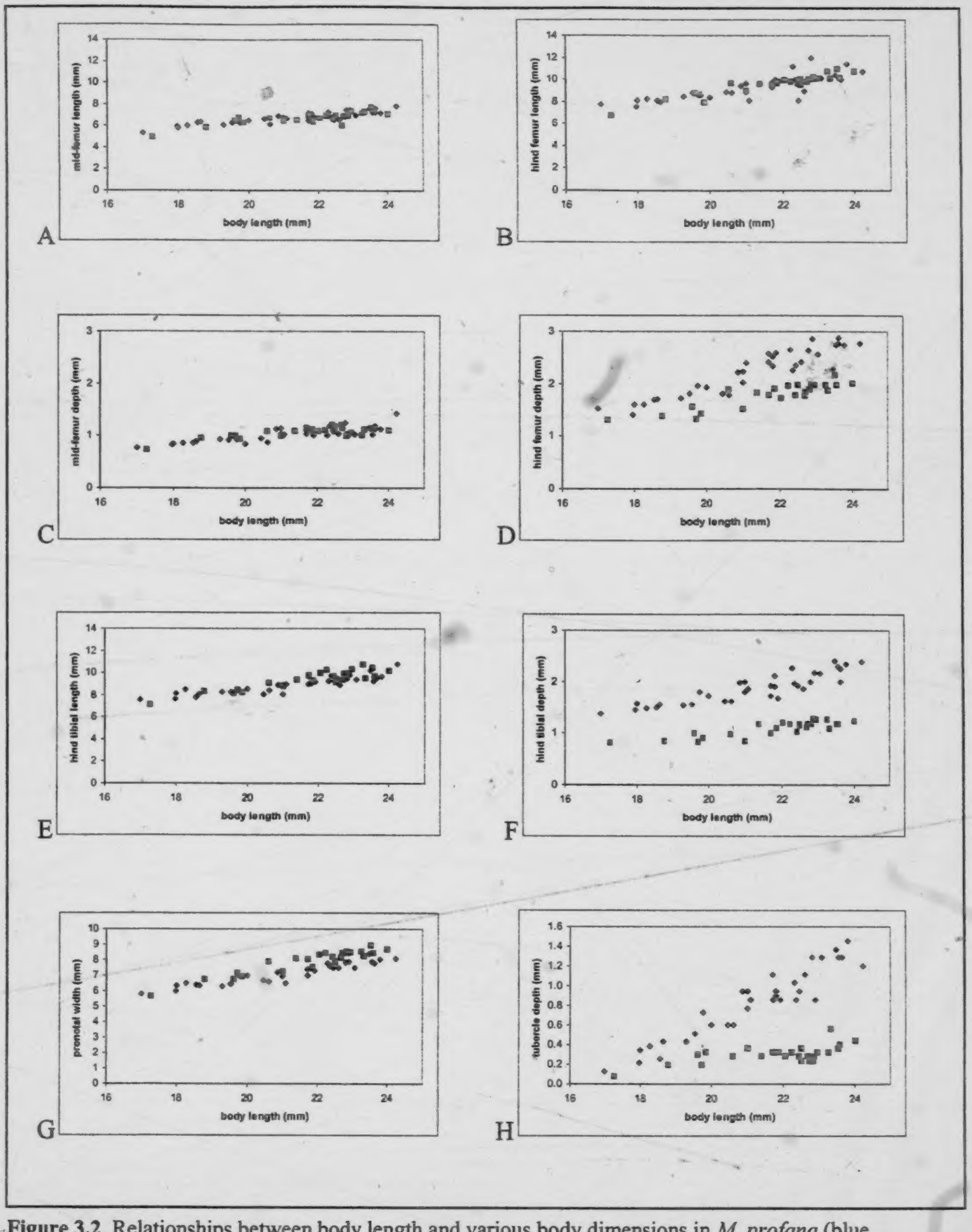

Figure 3.2. Relationships between body length and various body dimensions in *M. profana* (blue diamonds, males; red squares, females): A) mid femur length, B) hind femur length, C) mid femur depth, D) hind femur depth, E) hind femur length, F) hind tibial depth, G) pronotal width, H) tubercle depth.

Table 3.2. Log-log regressions of various body parts on overall body length in males (n=34) and females (n=25) of *M. profana*. For Student's t-tests of allometry (slope >1), LLR slopes have been converted to reduced major axis regression slopes (RMA) as discussed in Green (1999). Results of ANCOVA for sex effect are reported as t_{sex} and P_{sex}. Student's t-tests were also used to test for significant differences between male and female RMA slopes (for heterscedastic variables a modified t-test was employed, as described in Bailey 1997).

Structure	LLR slope± SE	r^2	RMA slope	$t_{allometric}$	$P_{allometric}$	t_{sex}	P_{sex}	t_{slope}	P_{slope}
Midfemur length									
Male	0.837±0.069	0.820	0.924	1.091	*ns*	-1.876	*ns*	0.770	*ns*
Female	0.910±0.127	0.690	1.096	0.752	*ns*				
Midfemur width									
Male	1.244±0.1321	0.735	1.451	3.415	<0.05	1.093	*ns*	0.546	*ns*
Female	1.001±0.171	0.600	1.292	1.715	<0.001				
Pronotal width									
Male	0.938±0.059	0.888	0.995	0.081	*ns*	8.281	<0.001	1.131	*ns*
Female	1.226±0.087	0.897	1.295	3.394	<0.05				
Hind femur length									
Male	1.015±0.123	0.679	1.232	1.879	*ns*	0.102	*ns*	0.340	*ns*
Female	1.250±0.091	0.891	1.325	3.561	<0.05				
Hind femur depth (max)									
Male	2.053±0.135	0.878	2.191	8.793	<0.001	-12.877	<0.001	1.603	*ns*
Female	1.565±0.169	0.789	1.761	4.515	<0.001				
Hind tibial length									
Male	0.797±0.071	0.800	0.892	1.531	*ns*	2.885	<0.05	1.102	*ns*
Female	1.087±0.098	0.843	1.184	1.876	*ns*				
Hind tibial depth									
Male	1.495±0.126	0.814	1.657	5.197	<0.001	-30.491	<0.001	0.353	*ns*
Female	1.495±0.191	0.727	1.754	3.943	<0.001				
Median Tubercle depth									
Male	5.733±0.361	0.888	6.086	14.102	<0.001	-16.459	<0.001	6.426	<0.001
Female	3.179±0.623	0.531	4.362	5.399	<0.001				

Table 3.3. Comparison between RMA regression slopes of wild-caught (n=12) and laboratory-reared (n=22) *M. profana* males. Wild male slopes and comparisons should be interpreted with caution due to many low r^2 values.

Structure	LLR slope± SE	r^2	RMA slope	t_{slope}	p_{slope}
Midfemur length					
Wild	0.931±0.336	0.434	1.413	1.427	*ns*
Lab	0.847±0.080	0.847	0.920		
Midfemur width					
Wild	1.671±0.571	0.407	1.451	1.947	*ns*
Lab	1.099±0.158	0.693	1.292		
Pronotal width					
Wild	1.459±0.246	0.778	1.654	2.789	<0.05
Lab	0.897±0.065	0.899	0.943		
Hind femur length					
Wild	1.630±0.796	0.225	1.232	1.519	*ns*
Lab	1.673±0.132	0.884	1.325		
Hind femur depth (max)					
Wild	0.839±0.550	0.188	2.191	0.654	*ns*
Lab	1.467±0.121	0.880	1.761		
Hind tibial length					
Wild	0.906±0.307	0.465	1.328	1.027	*ns*
Lab	0.956±0.0691	0.905	1.000		
Hind tibial depth					
Wild	2.254±0.619	0.570	2.986	1.169	*ns*
Lab	2.132±0.1153	0.906	2.240		
Median Tubercle depth					
Wild	3.554±0.925	0.888	4.602	1.752	*ns*
Lab	6.038±0.509	0.531	6.452		

Discussion

Sexual dimorphism and allometry

Body size is not sexually dimorphic in *M. profana*, although there is certainly dimorphism in the appearance of various structures and the relative scaling of these with body size. These relationships involve structures associated with sexual competition and behaviour and thus are explained by the evolutionary pressures of sexual selection (Chapter 4).

As expected, midfemur measurements and scaling relationships did not differ between sexes, since midfemora are not visibly dimorphic and do not appear to play any specific role unique to either females or males. Hindlimbs on the other hand are highly dimorphic between the sexes, and this is reflected in their scaling relationships. Males possess greatly enlarged and curved hind femora and ventrally armed hind tibiae which are used in male-male combat, while female hind femora are less incrassate and less curved, and hind tibiae are not armed with a ventral spine but instead possess a weak ventral leaf-like dilation. Similar to the results of Miyatake (1997), hind femoral length was not found to differ in either mean value or in slope between the sexes. Oddly enough, though mean hind femoral depth was found to be 18.8% dimorphic (Table 3.1) and there was a significant effect of sex (Table 3.2), both sexes expressed allometry in this character and slopes were found to be only marginally different ($p<0.052$) in contrast to the stronger results of Miyatake (1997). In *M. profana*, across all body sizes males tend to have significantly thicker hind femora, but this is not expressed to a disproportionately greater degree in large males than in large females. One likely explanation is that hind-limb depth (i.e., muscle mass) is indeed a genetically determined sexually selected trait, but it is not expressed exclusively in males. Thus the trait "large hind femur" is passed on not only to sons but to daughters as well, at least to some degree. This would be similar to what is seen in some stalk-eyed flies, where females to a lesser extent show the same enlarged eyespan tendencies as do males, upon whom sexual selection is acting (Wilkinson and Dodson 1997).

Hind tibiae are also visibly quite dimorphic between the sexes, and again this shows clearly in the data. Mean depth measured across the male tibial spine is 41.5% deeper than the depth of the tibial dilation in females. As with femoral depth, tibial depth is allometrically scaled in both sexes, and there is no significant difference between the slopes. Thus tibial depth also appears to be greater on average in males but shares the same relationship to body length as in females. In *Leptoglossus australis*, another coreid bug with similar hindlimb modifications, Miyatake (1997) found that the femoral characters alone showed scaling dimorphism and were important in male-male combat. Video-taped observations of *M. profana* however (discussed in Chapter 4), show that in this species at least, male tibial spines are also very important in fighting, and are used to slash at an opponent's hemelytra as well as for throwing opponents.

Of the structures hypothesized to be sexually selected, only the median abdominal tubercle showed significant differences in mean value, sex effect and slope. Because the median abdominal tubercle is really only present in males, these differences are to be expected. Differences in scaling relationships between hindlimbs and tubercle may also be linked in part to development and function. The primary function of hindlimbs is the same in both sexes (i.e., locomotion), and the development of hindlimb modifications is thus constrained with respect to development of the limb to also serve this primary purpose. Over five nymphal stages the legs gradually change, with secondary structures such as tibial spine and femoral dilation becoming more and more visible with each moult. The abdominal tubercle however, has no known function outside of the sexual arena, and is presumably not needed in any form in the nymphs. In fact, the possession of an abdominal tubercle in early developmental stages would probably be quite costly, as moulting of elaborate structures in insects can be difficult and even fatal. Also, if femoral depth reflects femoral muscle mass, the outer diameter will depend on how much muscle tissue the insect can accrue before its final moult. Conversely, the abdominal tubercle is hollow, and is therefore not constrained by muscle development within (the same could be said for the hind tibial spine). Perhaps then, the development of the median abdominal tubercle is withheld until the last possible moult, thereby freeing the insect of potential costs in that structure (e.g., potential difficulties in moulting and locomotion) throughout the five nymphal stages.

Wild vs. captive-bred males

Although wild-caught males were significantly larger in all respects than their lab-reared progeny, they nonetheless showed identical scaling relationships against body size. Because of this, we can justifiably pool both data sets to make inferences about scaling relationships exhibited in the wild. Overall small sizes in the lab population can probably be explained by environmental and dietary factors, particularly during the winter months, when the smallest individuals completed their development. During this time, it was nearly impossible to maintain high humidity levels in the growth chamber. As well, fresh produce in the form of snow peas and oranges was difficult to obtain. These factors, along with artificial grow lights in the place of direct sunlight and poor host plant condition probably placed a certain degree of stress on these individuals, thereby affecting their growth.

Variation about the mean

All of the measured traits that are believed to be under sexual selection (hind femur depth, hind-tibial depth and median tubercle depth) show significantly greater variance in males than in females ($p<0.05$: though once data are log-transformed, variation in tibial depth is no longer significantly different). There is some debate as to whether one would expect greater or lesser variation in traits under strong selection. If selection pressures are strong enough (and specific enough), it is argued that this may streamline character variability by exhausting genetic variation in the trait (Eberhard *et al.* 1998, Kirkpatrick and Ryan 1991), reducing overall variation. Conversely, it is also possible that sexual selection could favour alleles that convey greater variability in the given characters. Both scenarios may exist in different systems, although there is an increasing body of evidence suggesting that sexually selected characters do in fact show more variability (e.g. Pomiankowski and Møller 1995, Rowe and Houle 1996, Petrie 1992).

Eberhard *et al.* (1998) provide other plausible explanations for apparent increases in variation, neither of which invokes sexual selection on variance. First, if two characters are regressed on body size, they could share the same mean yet one might have a steeper scaling relationship than the other, resulting in a greater standard deviation. Likewise two regressions might share the same regression line, while one dataset might have greater dispersion than the other, again leading to a higher standard deviation. The first scenario argues for selection of a particular scaling relationship of the trait against body size, whereas the second scenario may result from genetic factors, environmental variation and imprecision in development.

Given this, it is difficult to determine what meaning, if any, can be attached to the increased variability in male secondary sexual characters in *M. profana*. If we return to the variance in hind femur depth measures (non-transformed), and the two log-log regressions against body size, we find that the male regression is higher than that of the female, yet slopes are identical. At least in this case then, differences in variance about the mean are not the result of different slopes, and so we can conclude that there is in fact more variability in this trait in males as compared to females.

Conclusions

For various reasons, it is argued that structures important in competitive displays and intrasexual competition should show positive allometric growth patterns (e.g. Petrie 1988), because it is not cost-effective for smaller, less competitive animals to invest as much energy into these characters as their larger, more competitive conspecifics.

Characters involved in mate choice should also show this pattern, either for the same reasons as above, or because smaller individuals might in effect be of poorer condition, in which case smaller trait size becomes an honest measure of that individual's quality (Green 1992). To confound matters, if competitive display/ fighting traits are a true reflection of an individual's phenotypic (and underlying genotypic) condition, then such characters might also become the target of direct mate choice (Petrie 1992).

In *M. profana*, males have significantly thicker hind femora than females, and sharp hind tibial spines which are deeper than the corresponding tibial dilations in their female counterparts. Both traits scale allometrically with body size, yet neither of these characters shows sexual dimorphism in slope. Only median abdominal tubercle measures show dimorphic scaling with males exhibiting much steeper scaling than females. However, all three of these characters are heteroscedastic, with males being much more variable than females.

These scaling relationships alone do not tell us how males compete, how females choose mates, or any of the underlying selective forces that have sculpted the intriguing structural variation we see today. For this we need to look at the behaviour of the animals themselves, and this is the subject of the next chapter.

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Chapter 4

Reproductive and fighting behaviour in *Mictis profana* (Hemiptera: Coreidae) and allometric scaling of male secondary sexual characteristics

Introduction

Specific characters that confer a mating advantage to some individuals over others are said to be under sexual selection, a term first coined by Darwin in *The Descent of Man and Selection in Relation to Sex* (1871). Darwin envisioned this as differing from Natural selection in that many of these characteristics are in fact maladaptive in everyday life (e.g., the long, elaborate tail of the peacock, though attractive to pea hens, is costly to produce, cumbersome to drag around, and a hindrance when fleeing a predator: Zahavi 1975), nonetheless, their overall reproductive benefits are so strong that they persist and even flourish, becoming ever more elaborate (Fisher 1930). Sexually selected traits may function in intra-sexual competition, or they may be under direct mate selection. In certain cases where combat or competitive characters are a true representation of an individual's fitness (e.g. Maynard Smith 1982), then these also become the target of direct mate choice (e.g. Kodrick-Brown and Brown 1984).

Whereas males generally attempt to mate more frequently and are less selective of their mates, females are generally more selective, tending to prefer certain males over others. It is presumed that such choosiness reflects the relative energetic input of the respective sexes into their progeny: those individuals who elicit the greatest cost in reproduction (e.g. the energetically expensive production of eggs by females versus the relatively cheap production of male sperm; the costs of parental care by a single parent: see Trivers 1972) will thus have the most to lose in mating, and so will put more effort into selecting the best mate possible. There are also factors other than getting the best value from a mating which may influence female receptivity. Depending on various factors, the act of mating itself can be costly to an individual, regardless of the quality of the potential mate. This cost is often manifested as an increased risk of predation (e.g. Arnqvist 1989) or as a decrease in foraging ability (e.g. Stone 1995) or ability to oviposit (Spence and Wilcox 1986). In the solitary bee, *Anthophora plumipes,* for example, male harassment forces females to forage at less optimal foraging sites (Stone 1995), while in the African swallowtail butterfly, *Papilio dardanus,* male harassment is so debilitating that some females have adapted male-specific colour patterns in order to avoid detection by conspecific males (Cook *et al.* 1994). In the end there are many reasons why an individual may choose not to mate, and it is up to the suitor to find whatever way possible to overcome such reluctance, either by displaying his value (true or apparent) or by other (even forcible) means (e.g. Spence and Wilcox 1986).

In the leaf-footed bug *Mictis profana*, males possess enlarged hind femora and spined hind tibiae, both of which are believed to function in male-male combat as observed in other coreids (Mitchell 1980, Miyatake, Eberhard 1998). In addition to this fighting armature, males are also endowed with prominent lateral and ventral abdominal tubercles situated on the margin of the 3rd and 4th abdominal sternites, the function of which has never been studied. These abdominal tubercles show highly allometric growth in relation to overall body length (Chapter 2).

As in other coreids, males also possess a ventral abdominal gland (VAG) which opens midventrally in the 7-8th intersegmental membrane and releases volatile compounds (Aldrich *et al.* 1982). Based on analyses of several species, these VAG secretions appear to be species-specific blends of aromatic alcohols (Aldrich *et al.* 1976) but their function is presently uncertain.

After a brief description of general biology and behaviour of *M. profana* based on field and laboratory observations, this chapter explores how various aspects of *M. profana* behaviour relate to morphology and sexual selection. Fighting and mating behaviours for this species are described and illustrated for the first time, and the possible functions of the median abdominal tubercle and the VAG are explored. Assortative mating with respect to male body size is shown, and the potential costs of mating incurred by females are then tested by exploring how male presence affects female foraging.

Materials and Methods

General biology, fighting and mating behaviour

All field observations were made between January 8th and March 12th 2002 at the Koronivia Field Station of the Ministry of Agriculture Fisheries and Forests (MAFF), Viti Levu, Fiji (S 18^0 02' 52.5", E 178^0 32' 15.0", 3m elevation). Crusader bugs were observed in a crop of approximately 50 Pigeon pea plants (*Cajanus cajan*) which had been planted the previous year in a c. 465 m^2 plot. General life history observations were made of both captive and wild insects. Insects used in mating studies were kept in outdoor mesh enclosures (2.5 × 1.5 × 2 m.) erected over live pigeon pea plants. These were monitored four to seven days per week, and were periodically moved to new locations whenever the host plants showed signs of stress (excessive feeding damage, mould, wilt).

Individual insects were labelled with yellow model paint on the front of the pronotum: letters for females and numbers for males. To examine mating patterns among individuals, two separate enclosures approximately 5m. apart were populated with marked individuals. In total, four scan-sampling series were undertaken. These were conducted on the following dates: March 1-6, 2002 (7 males and 5 females in Enclosure I, 7 males and 4 females in Enclosure II) and March 6-8, 2002 (switching females between Enclosures I and II). The mating behaviour of each individual insect was recorded each day over half-hour intervals, beginning within one hour of sunrise and lasting a minimum of three (7 scans) and a maximum of four hours (10 scans) per day. Observations were limited to this schedule because of the daily tropical showers, which began in the late morning or early afternoon. If two insects were seen mating over more than two consecutive scan samples, this was considered a single mating event. Back in the laboratory, various body measurements were taken using an ocular micrometer and Vernier callipers.

A colony of *M. profana* was then brought back to the University of Alberta for continued study. These were maintained in a growth chamber with 12L:12D photoperiod and 60-80% humidity. Insects were fed live pigeon pea (*Cajanus cajan*), sliced oranges and washed, store-bought snow-peas. Oranges were placed on stakes approximately 30 cm. tall, while peas were hung from the plant and the mesh walls of the cage using bent insect pins. Thirty mating attempts (including unsuccessful attempts and several incomplete sequences) and four fights were videotaped using a Canon A1 Digital Hi 8 camera, with a 2X magnification lens.

To examine the function of the VAG, abdominal stretching behaviour (discussed below) was used as an indicator of gland use, and scent glands were removed at various times from dead insects, their contents introduced into insect enclosures, and behaviours noted.

Mate harassment

To study the effects of male presence on female foraging behaviour, three randomly chosen females were introduced into a cage (38 × 38 × 74 cm) containing a single young pigeon pea plant with one main branch and very little new growth. The females were allowed ten minutes to settle themselves, at which point a single male was introduced onto the plant near its base, and the behaviours of all individuals were recorded. This was repeated 4 times with different sets of insects. As a control, the entire experiment was repeated with the introduction of an additional female instead of a male.

Results

General behaviour

As with other coreids, *Mictis profana* is known as a "tip-wilter" because of the kind of damage it causes, and feeds mostly on the fruits and young shoots of its host plants (Schaefer and Mitchell 1983, Schaefer and O'Shea 1979). In Fiji it is considered a pest of eggplant and cowpeas (Waterhouse 1997). It also feeds on citrus fruits, and is occasionally found in very high densities (Sada Lal, pers. com.). When disturbed, these bugs sometimes eject a stream of clear liquid from the abdomen and, like other coreids, they also release potent defensive compounds from the metathoracic scent glands in adults, and dorsal abdominal glands in nymphs. On more than one occasion, freshly captured insects died either within the containers in which they were transported from the field to the laboratory or even in the sweep nets used for their capture, presumably succumbing to their own defensive secretions (personal observations).

The terminal antennal segments of nymphs and adults are bright yellow, and were sometimes vibrated vigorously when the bugs were disturbed. This may distract potential attackers away from the insect's body, may be an aposematic warning signal, or perhaps may even function as wasp mimicry, with the coreids imitating similar behaviours of sphecoid wasps. Mimicry of hymenopteran behaviour and appearance is quite common among Heteroptera, and at least one other family in the Coreioidea- the Alydidae- is well-known for both structural and behavioural mimicry of this sort (Schuh and Slater, 1996). The probable selective importance of this trait is underscored by my observations that if the terminal segment is removed from an early instar nymph, the penultimate segment will instead become brightly coloured (pers. obs).

Nymphs are black with bright orange colouring, likely an aposematic warning. Adults, though mostly brown, are also adorned with a bright orange abdomen, which is exposed when the insects take to the wing. This may also be a case of wasp mimicry, as the bright orange colouring and loud buzzing sound of their flight lends these bugs the appearance of large sphecid or pompilid wasps.

During field experiments, wild bugs were frequently seen gathering near outdoor test enclosures. This was especially true on days with a very gentle breeze, when both males and females could be observed approaching from downwind, flying from plant to plant. These bugs would eventually land directly on the mesh enclosures, and in a few cases probe through the mesh with their probosces as though they were trying to feed. In all cases wild bugs were attracted to enclosures containing both males and females; in no case were they seen approaching an enclosure harbouring only females, which was maintained for one week.

Ventral abdominal gland

Many males were seen perched upside-down at the tops of their host plants, usually with their legs spread apart and their terminal abdominal segments extended, thereby exposing the opening to their VAG, a position I call abdominal stretching. Abdominal stretching was exhibited by lone males as they fed, by males as they were courting females, and even by males just prior to combat. Seldom would only a single male engage in abdominal stretching; generally in a cage or enclosure all males of breeding age would do so in concert. Twice males were observed stroking their VAG openings with their hind tarsi then rubbing them together. At no time did it appear that a male deliberately touched his VAG opening to a female during courtship.

When VAG glands were dissected from recently deceased insects they released a very strong smell, reminiscent of apples. Three times VAG contents were introduced into indoor enclosures with inconclusive results. In all instances insects within the enclosures appeared immediately aware of the new smell, indicated by deliberate antennal movements directed towards the source. Twice several males and females wandered about the enclosures as though searching out the source of the VAG compounds, though this behaviour lasted only a few minutes. In one case a male who had been sitting quietly began to quickly walk about the cage, and within a minute began to successfully court the first female he encountered. In the last case no unusual behaviour was recorded aside from antennal waving.

Male body size and mating

During day to day scan samples, many males were seen in the same location from one day to the next, although exact daily locations were not specifically recorded. The same trend was seen in the laboratory, with the largest males appearing to defend preferred food sources. When data from both enclosures were pooled together, the amount of time spent in copula (measured as the number of times an individual was seen mating) and the number of mating events per individual were both positively correlated with male body length (Pearson Product Moment Correlation, $P<0.05$), whereas the total number of mating attempts and total number of female partners per individual were not. All but one male was seen mating at least once. A summary of pooled results is shown in figure 4.1.

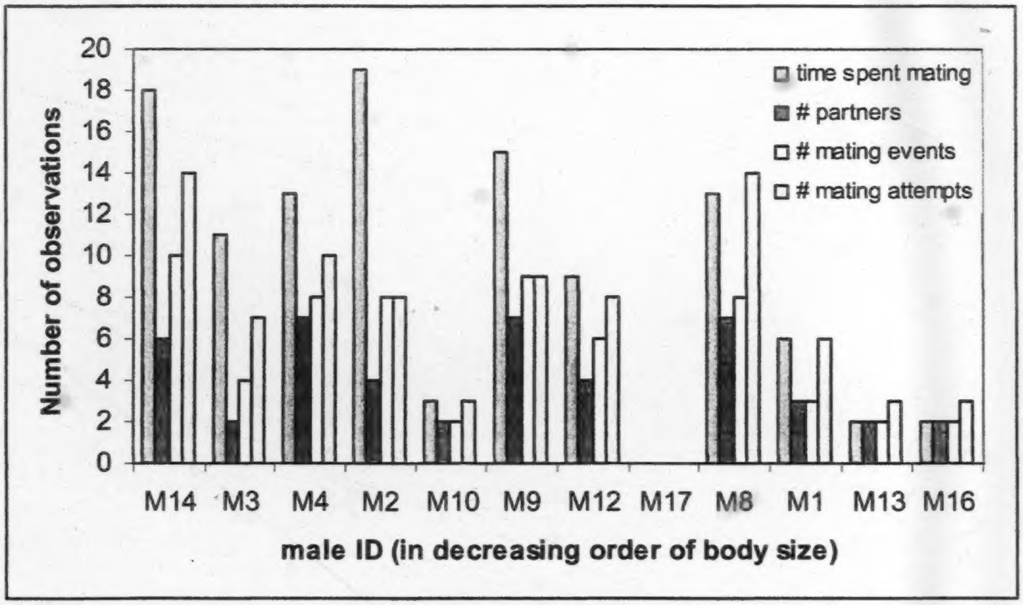

Figure 4.1. Pooled observations from scan samples of mating behaviour of *M. profana* (March 1-6 and March 6-8, 2001). Observations include: total number of partners per male, total number of matings observed, total number of mating attempts (whether successful or not), and the amount of time spent mating. This last observation is recorded as the number of times an individual was seen mating, regardless of whether this was a continuation of a previous mating event or not.

Mating behaviour

In the field, matings were observed within the second hour after sunrise, through the day and into dusk. In captivity, where day and night temperatures were held constant, mating was observed mainly in the lights-on period, but occasionally couples were found in copula within a few hours after dark. Both males and females mated with multiple partners, sometimes having several partners in a single day.

Of thirty videotaped mating attempts, eighteen resulted in the male mounting the female, and fourteen of these resulted in successful copulation. Courtship lasted from less than a minute to over twenty minutes, though no courtships that lasted more than 5 minutes ended in successful copulation. In all but two successful mating attempts the female was already feeding when approached by the male. In contrast, only three of the failed courtships involved feeding females. Four additional mating attempts were recorded where a male tried unsuccessfully to mate with a female who was already in copula.

Mating in *M. profana* is initiated by the male, and is similar to that of other coreids (e.g. *Acanthocephala declivis guatemalana*, Eberhard 1998; *Mictis tenebrosa*, pers. obs.). The sequence is described as follows. The male almost always approached the female from the front or the side (N=23), and as soon as he contacted her with his antennae he typically paused, sometimes for over one minute (Fig. 4.2a). The male then drew nearer and began to mount the female's dorsum. In seven of the 30 taped courtships males approached and attempted to mount from behind. This behaviour was met with resistance every time, with the resistant female raising her hindlegs, kicking at the would-be suitor and attempting to flee. Males sometimes chased retreating females, but were never able to secure a successful mating in this manner.

The following behaviours were observed in all eighteen videotaped mountings. Once on a female's back the male turned to orient himself to face the same direction as the female, curled his antennae down over her head and drew his hind tarsi up high, so that they were almost beneath his median abdominal tubercle (Fig. 4.2b). In this position the male tapped quickly and repeatedly on the female with his hind tarsi, while at the same time rubbing his median tubercle over the female's back. Tubercle rubbing was often jerky and imprecise yet appeared deliberate, as the male seemed to draw his body forward much lower than during normal locomotion. In extended courtships males walked about on the female's back, sometimes turning to face in the opposite direction, but ultimately returning to face the same way. After a period ranging from less than 10 seconds to a minute, the male moved off to the female's side with his median tubercle pressed against the lateral margins of her abdomen. From this position he rubbed forward and backward along her side; two males were observed to do this with quick and rhythmic jerking movements. In this position the male then attempted to reach around the tip of the female's abdomen with his genital capsule and join his genitalia to hers. In six of the 14 successful matings, males were able to make genital contact in the first attempt. In all other attempts the male was forced to return to the female's back and continue courtship.

Eventually the tip of the female's abdomen began to pulse slightly at a frequency a little quicker than once per minute, presumably indicating her readiness to mate. When attempting intromission, the male extended his genital capsule outwards and to the side in such a way that its dorsal aperture was facing the female's genital pore. On two occasions where males were significantly smaller than females this proved to be quite difficult, as the males were unable to reach their respective partner's genitalia from their position on her dorsolateral margin, and so could not achieve copulation. Usually after several attempts, the genital capsule was brought into contact with the female's genital pore, his pygophore angled straight upwards. As the genitalia were inserted and copulation began, the tip of the female's abdomen pulsed more strongly. Upon successful intromission, the male then dismounted and realigned himself either off to the side or facing directly away from the female, his genital capsule twisted and nearly upside down (Fig. 4.2c).

Throughout courtship and into copulation the female continued to feed; males too would sometimes feed, if their location permitted it. Occasionally couples were seen moving about, the female leading the way and the male in tow. Mating lasted as little as 1-2 minutes (though whether sperm transfer was successful in these cases is extremely doubtful) but usually lasted at least one hour, up to a recorded seven hours. Additionally, several male-female pairs were frequently seen together over the course of consecutive days, sometimes mating but often simply sitting side-by-side. Mating was usually terminated by the female, who would gently touch, push or rarely kick at the tip of the male's abdomen with her hind tarsi, and the pair would separate. Matings were often interrupted by other males (rarely females), who attempted to court the female. This was recorded on video four times: in all cases the interloping male courted in the normal fashion, apparently unaware that the female was already with a mate. During three of these interruptions both the mating male and female tried to ward off the interloper, with the confrontation eventually escalating into high intensity male-male combat as described below. In the last interrupted mating, the courting male was ignored. Illustrations and a flow chart depicting the mating sequence in *M. profana* are shown in Figures 4.2 and 4.3 respectively.

Twice after a female had rejected a suitor and fled the area, males continued their courtship behaviour directly on the substrate where the female had just been. One male was observed rubbing his median tubercle and tapping vigorously on a snow-pea for approximately five minutes after his would-be mate had fled. Once a male was seen mounting a nymph, and twice males were seen mounting other males while they themselves were courting. Four times this behaviour was experimentally induced in different individuals, both by physically removing the female from a copulating/ courting pair, and by removing the male and placing him near other individuals.

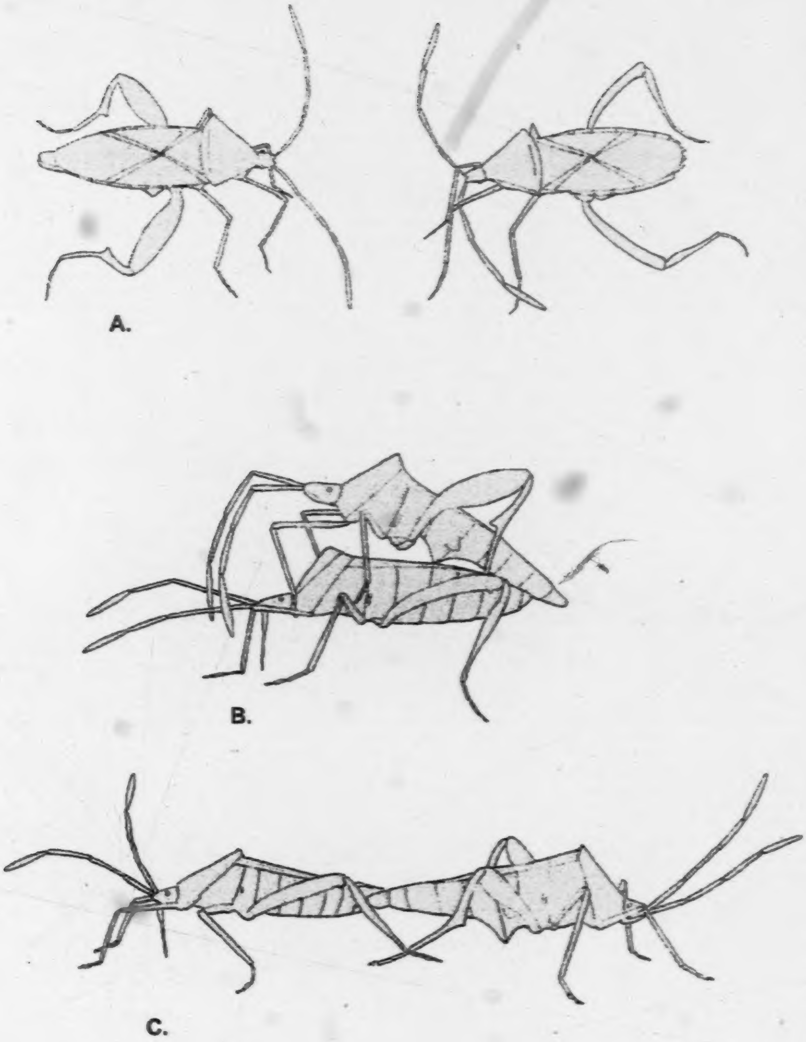

Figure 4.2. Illustration depicting various stages of *Mictis profana* mating behaviour. In A) the male (brown, on the left) approaches the female (green) and pauses. B) Shows the male already on the female's dorsum with his antennae angled down over the female's head, his hind tibiae up high and his median abdominal tubercle pressed against the female's body. Once copulation begins, the male dismounts and turns to face the opposite way, as shown in C).

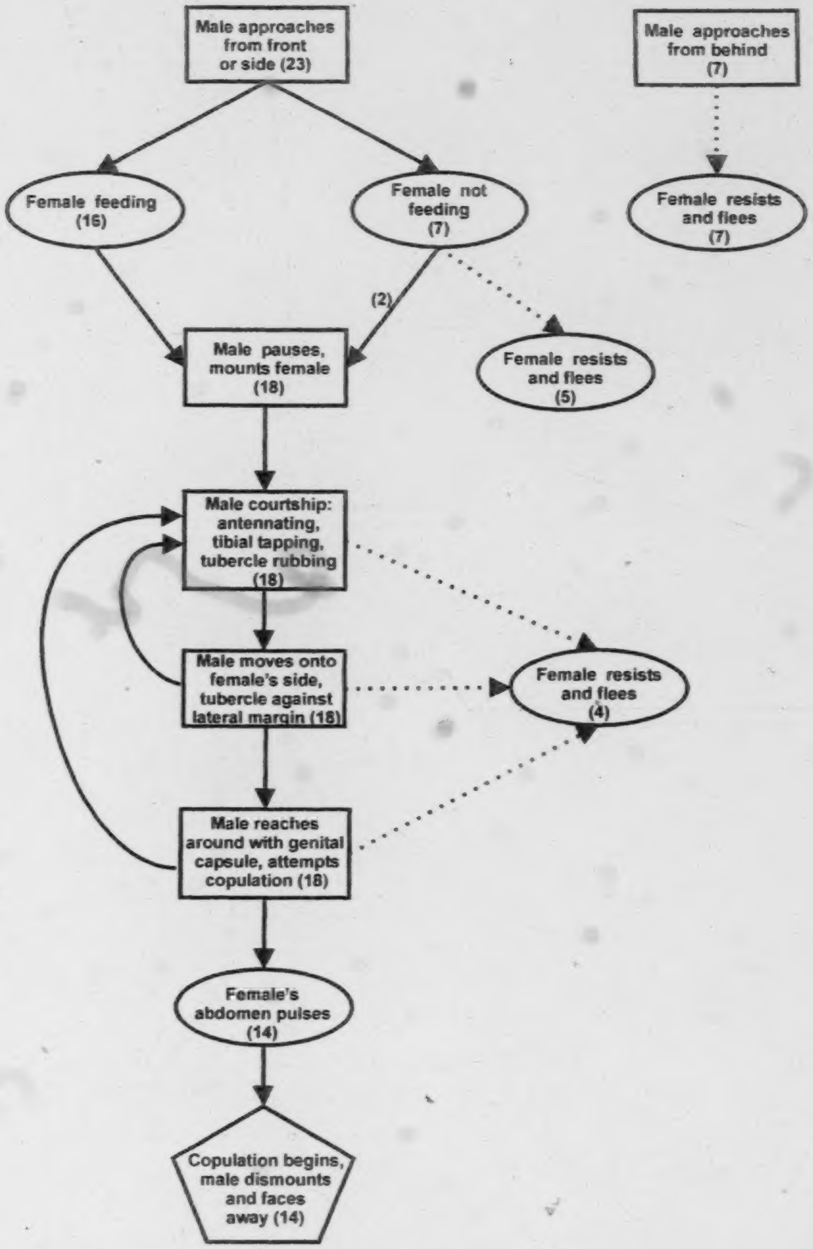
Male approaches from front or side (23)
Male approaches from behind (7)
Female feeding (16)
Female not feeding (7)
Female resists and flees (7)
(2)
Male pauses, mounts female (18)
Female resists and flees (5)
Male courtship: antennating, tibial tapping, tubercle rubbing (18)
Male moves onto female's side, tubercle against lateral margin (18)
Female resists and flees (4)
Male reaches around with genital capsule, attempts copulation (18)
Female's abdomen pulses (14)
Copulation begins, male dismounts and faces away (14)

Figure 4.3. Flow chart depicting the mating sequence in *Mictis profana*, based on 30 videotaped courtship attempts. Numbers indicate how many times a given behaviour was recorded. At virtually each step of the sequence females have been observed either resisting or fleeing from male advances.

Agonistic behaviour

Physical conflict in *M. profana* has been observed in both sexes, even between early instar nymphs, and spans a range of intensity. In the simplest form of aggressive display, one individual runs at another and chases it away. If the confronted individual does not flee, conflict ensues. Low-intensity conflict was generally associated with access to feeding locations. When a feeding insect of either sex was approached by another, it would often raise its hindlimb nearest to the interloper as if in warning. If the invader continued to approach, several blows of slow to moderate speed would be delivered: these often elicited a like response, with the defender and invader jousting for several seconds. Such behaviour was seen in adults and even between nymphs as young as second instar.

More intense combat almost exclusively involved males. These fights involved access to feeding sites, when one male disturbed a mating couple, or when two or more males were both attempting to court the same female. These fights sometimes ended quickly, though in one case two small males were seen to fight vigorously for ten minutes. In all four videotaped bouts, when two males were about to engage in conflict, they would sidle up to one another facing the same way, bodies parallel. Fights began with one male raising his hindlimb nearest the opponent and striking out and downwards, while at the same time the defender would respond by raising his hindlimb to block and counter-strike. After perhaps 5-10 seconds of this moderate-intensity fighting, the battle sometimes ended with one or the other insect running away from further combat. If both males were of similar size, the fight was likely to escalate to a high-intensity bout.

The highest-intensity bouts were generally seen between males of large and similar size. This type of combat was videotaped four times; twice involving males who had been interrupted during mating, and twice apparently stemming from a territorial dispute. In these battles males approached one another as above, bodies parallel and facing the same way. Males would strike out with their hind legs and attempt to grasp their opponent, at the same time rotating their venters inwards and wrapping their legs around one another in a tight embrace. With hindlimbs locked around each other, males alternated between squeezing and striking their opponent's dorsum with both hindlimbs, with the tibial spur sometimes striking the hemelytra and abdomen of the opponent. These blows were extremely quick and powerful, and generated a loud snapping noise. It is not clear whether these fights regularly caused significant damage, though one videotaped bout clearly shows the tibia of one male tearing through the lateral margin of his opponent's hemelytra, and several males in the field and in captive populations had tattered wings. In a study of *Acanthocephala declivis guatemalana*, another coreid with similar fighting behaviour, Eberhard (1998) noted that males often showed substantial wing damage from combat.

In two videotaped fights, grappling males were observed swaying side to side, in one case thrashing violently back and forth. This was apparently the result of the male who's hind legs were pinned by his opponent trying to break free. Males constantly struggled to get their legs overtop of their opponents', at which point they would deliver a powerful squeeze that would rock both individuals, knocking them off the plant in two cases.

Even with high-speed video it was difficult to tell what role male abdominal tubercles might play in these contests. Most of the time the tubercles were obscured behind the hindlimbs, so their ~~role~~ could not be accurately assessed. However, in two videotaped fights the tubercles did in fact make definite contact with the opposing male.

Twice when two males were grappling, one male was observed using his tibial spine, which is angled down towards the tarsi, to pry the opponent away. This was done by hooking the spine under the lateral margins of the abdomen or onto the opponent's hindlimb and forcibly pushing outwards.

While fighting was most commonly seen in males, females were also sometimes quite aggressive. In one case, a female who had recently terminated mating with a particular male, was seen to approach her former mate as he was courting another female and violently kicked at that female until courtship ceased.

Mate harassment

Effects of male presence on females were nearly identical in four independent sets of observations. When first introduced into the cage the three females always proceeded immediately up to the new growth at the top of the pigeon pea plant. Females showed very little aggression towards one another, although in one trial two females engaged in minor fighting over access to the most apical new growth of the plant. Within a few minutes the females had spread out over the terminal shoot of the plant.

Each time a male was introduced he too made his way directly to the apex of the plant. In all four trials as the male approached the first female encountered along the way, she would invariably move to avoid him. Eventually, as the male made his way to the tip of the plant, all the females dispersed away, either moving out to less central shoots or farther down the plant. In two cases where the male approached, the non-receptive female responded by leaving the plant altogether.

Results from the control group were also identical each time, with the new female progressing to the apex of the plant and settling near the top, and only minor aggression between her and any of the original females.

Discussion

Mating behaviour

As shown in figure 4.1, male mating success was non-random in *M. profana*, with larger males securing more matings and mating for longer periods of time. Whether this was the result of direct female choice, inter-male competition, or the physical inability of small males to successfully mate in the field enclosures is not known. Nonetheless, detailed observations of behaviour show that courtship does exist in *M. profana*, meaning that female choice is very likely involved. Although males frequently tried to mate with unwilling females, it was the female who ultimately decided whether mating would occur.

In every successful mating observed the male paused before mounting, antennated the female's head, tapped on her body, and appeared to rub his tubercle on her dorsum and sides. Sometimes these behaviours were extremely brief, other times they were repeated and lasted for several minutes. Because these behaviours were so consistent, I regard them as essential components of courtship behaviour in *M. profana*. How the female assesses male courtship behaviour remains unknown, but it is possible that both physical and chemical cues are essential. Possibilities of both are discussed below.

Males were often seen in the same location during successive days, with the largest males frequently defending food sources. This is evidence that *M. profana* uses a mating system characterized as resource defence polygyny. However, as in other insects (e.g. Spence and Wilcox 1986, Wilcox and Spence 1986) successful matings are not likely restricted to males that defend these sites. Some males and females were also observed moving about quite freely and prolonged mating and mate guarding was rampant (discussed below), suggesting that not all males defend territories, and may in fact rove about in search of females, thereby leading to male-male encounters and female harassment.

The unusual behaviour of misdirected courtship bears some discussion. These misguided mating attempts occurred immediately after failed mating attempts, when mating/courtship is interrupted, or with another male that was already mating, which suggests that contact pheromones play some role in courtship. It is probable, for example, that male courtship depends on positive feedback from stereotyped behaviours and cues given by the female. Once exposed to a specific signal, male behaviour might become constrained temporarily to a certain stage in the courtship cycle, even if the cycle is broken. If a receptive female were to produce pheromones on contact, even after her removal residual pheromones might remain on male receptors. This would explain why a male whose mate is removed goes on to court the pea she was feeding on, or attempts to mate with the nearest individual at hand.

Other studies of related insects suggest that both male and female pheromonal signals are often involved in courtship (e.g. Wang and Millar 2000). In the coreid *Riptorus clavatus*, for example, removal of terminal antennal segments precluded courtship initiation, presumably because individuals could not sense the cues being sent by their would-be mates (Numata *et al.* 1986).

Harassment and resistance to mating

Almost all non-feeding females resisted mating. In contrast, almost every time a mating was successful the female was observed feeding or within reach of food. This is similar to Stone's observations of foraging in the solitary bee, *Anthophora plumipes*, where male harassment forced females to forage at less optimal foraging sites (1995). Likewise, Ortigosa and Rowe (2002) have shown that in the water strider *Gerris buenoi*, starved females were much more resistant to mating that well-fed females. Resistance to mating is costly in terms of energy expenditure (Watson *et al.* 1998), reduction of feeding or foraging opportunities, inability to search out oviposition sites (e.g. McLain and Pratt 1999) and in some cases may increase the risk of predation (Rowe *et al.* 1994). Male presence or approach consistently prompted females to leave the terminus of the plant, and since bugs prefer to feed on the new growth at the tops of plants, mating pressure from males probably hinders female foraging behaviour. Thus, in *M. profana*, female mate choice may only be partly determined by male quality, with female hunger level also likely as a driving factor.

Mate guarding

While Eberhard (1998) did not find any evidence of mate guarding in *A. declivis guatemalana* it would appear that some degree of guarding does occur in *M. profana*, based on observations of prolonged mating and of males remaining in close proximity of to recent mates. Sperm transfer can almost certainly be completed in much less than seven hours, and prolonged mating is probably used by males to limit re-matings before egg laying, as in other bugs (e.g. Spence and Wilcox 1986). It is also possible that excess time spent mating may be used by males to manipulate rival sperm, though I have not seen any other behaviour or genitalic structures to suggest this. Since males were never observed engaging in any particular behaviour while mating other than feeding, copulatory courtship and cryptic female choice (Eberhard 1994) are unlikely causes of prolonged mating.

From the female's perspective, prolonged mating can also be adaptive, if courtship harassment is limited (Wilcox 1984). Evidence that females are willing participants in prolonged copulation comes from my observation that females are almost always the sex to end copulation, generally by gently pushing away from the male with their hind tarsi. As shown above, mate harassment by males of *M. profana* can affect female foraging ability, with females forced into suboptimal foraging areas in their attempts to avoid male contact.

Agonistic behaviour

In Chapter 2, male hind femoral width, tibial depth and abdominal tubercle depth were shown to scale allometrically to body length in males. From the behaviours described above, we can reasonably conclude that incrassate hind femora and tibial spines in males function in male combat. Sexual selection is likely the driving force behind the scaling relationships of these structures, with the largest and strongest males defending the best territories, winning the most contests and securing the most matings. It is not clear whether abdominal tubercles also play a role in male-male combat.

Function of the ventral abdominal gland

Because wild insects of both sexes were attracted to enclosures housing males, it is probable that VAG secretions act as an aggregation pheromone. These observations concur with Yasuda (1990), who showed that nymphs and adults of both sexes of the coreid *Leptoglossus australis* were attracted to adult males. Aldrich *et al.* (1999) suggested that in resource-based mating systems, aggregation pheromones are used by males who colonize a new host patch to attract potential mates. Since abdominal stretching in *M. profana* was observed during courtship, before fighting, and when males sat alone, it is possible that the VAG secretions are a part of male display behaviour, both as a signal of willingness to mate and as a display of territoriality to other males.

Conclusions

Mating success in *Mictis profana* depends on a complex set of interactions. Males defend food sources and may signal their presence through pheromones. Insects of both sexes home in on these signals, either in anticipation of the availability of food, in search of mates, or both. Male-male encounters may escalate into high-intensity physical matches, where large males with strong femora and large tubercles prevail. These males attempt to mate with feeding females, who sometimes resist their advances. When courting, the males engage in a series of stereotyped behaviours, including tubercular rubbing and tibial tapping, which elicits some sort of response, possibly in the form of contact pheromones, from the female. Eventually copulation begins, and couples engage in prolonged mating, which protects the male's reproductive interests as well as possibly limiting male harassment of females, thereby allowing them to feed uninterrupted. In this environment sexual selection drives male structure and behaviour, as well as female choice.

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Chapter 5

The biology and natural enemies of *Mictis profana* on Pigeon pea (*Cajanus cajan*) in Fiji

Introduction

The Crusader bug, *Mictis profana* (Heteroptera: Coreidae) is found throughout Indonesia, New Guinea, Australia and the South Pacific. In many parts of its range it is a pest of significant economic importance. In Papua New Guinea, for example, it feeds on Poinciana (Flanagan 1994), pigeon pea, *Cajanus cajan*, (Young 1984) and *Acacia aulocarpa* (Waterhouse 1997). In Australia it attacks citrus, cowpeas, green gram, *Eucalyptus*, *Acacia* and *Casia* (Flanagan 1994, Hely *et al.* 1982, Shepard *et al.* 1983). *M. profana* also attacks *Acacia alocarpa* in New Caledonia, while in Fiji it is considered a "widespread and important" pest of eggplant and cowpeas (Waterhouse 1997). Yet despite its considerable economic impact, the basic natural history of *M. profana* has received very little attention.

Short-term relief from crop pests can be achieved through the use of pesticides, however more often than not this comes at the cost of non-target species such as pollinators and natural insect predators and parasitoids, as well as contaminating the local food web, soil, water air, and even the very crops they are protecting (Altieri 1994). Biological control, the use of natural biological agents such as parasitoids and predators to control pest species, is an alternative that may help tropical farmers minimize the potential health risks and costs associated with pesticide use. The goals of this study were to search for any parasitoids or predators of *M. profana* and to understand aspects of the life history of this bug that might prove useful for its management.

Materials and Methods

At the Koronivia Research Station, Viti Levu, Fiji, a 464.3m^2 pigeon pea plot, consisting of approximately 830 plants, was found to harbour a healthy population of *M. profana*. This plot had never been sprayed with pesticides and remained unsprayed for the duration of this study. Adults, juvenile insects of various instars, and eggs were found throughout this plot for an extended period (December 2000 – March 2001), implying that *M. profana* breeds throughout the year on these plants.

Parasitoids and Predators

To study the possible egg parasitoids of *M. profana*, eggs were placed in the field for a minimum of one day and a maximum of five days (average=2.71 +/- 1 days). A short exposure period was deemed necessary to minimise the loss of eggs to avian and other predators. Because of the difficulty of finding eggs in the field, several live colonies were kept in confined enclosures indoors, ensuring a steady supply of eggs for the duration of the study. These insects were fed on fresh pigeon pea cuttings, which were replaced every two days. Additionally, any eggs found in the field enclosures were collected immediately upon discovery. (The mesh size of these outdoor enclosures was large enough to allow easy access for parasitoid wasps and small insect predators).

Of a total of 267 eggs reared during this project, 161 were exposed to the threats of parasitism and predation. Chains of eggs were attached deep within pea plants using dark coloured thread. This protocol was followed from Jan. 11th until March 12th, 2002. After exposure, eggs were collected and placed in 200 mL sample vials with perforated lids. Eggs were monitored daily for the emergence of either parasitoids or Crusader bug nymphs, and the dates of hatching and number of individuals were recorded.

While in the field, all incidents of possible predation were recorded. As well, the outdoor enclosures described above harboured many predatory arthropods and kept them in close proximity to many Crusader bug adults, immatures and eggs. On several occasions generalist predators (carabids, spiders and big-headed bugs) were placed in smaller enclosures with Crusader bug nymphs for temporary observation. Because of defensive chemical secretions, coreids are not expected to suffer significant predation or parasitism (Steinbauer 1999, Steinbauer & Davies 1995.) For this reason, it was expected that any predation observed would likely be on eggs rather than on nymphs and adults.

Results

Part of the Crusader bug's effectiveness as a crop pest is due to its polyphagous feeding habits which extend across several plant families. Marked insects transplanted from a nearby eggplant patch to the experimental pigeon pea plot, for example, readily fed on the pigeon peas, and remained in the same location for several days.

Crusader bug eggs are small and cylindrical, about 2.7 mm in length. These were laid either singly or in chains of between 2 and 15 eggs, with an average of 4.34 +/- 3.06

eggs per clutch. Eggs possessed a small operculum on the dorsal surface, through which nymphs emerge. The eggs were covered with a white powdery substance of unknown function. Eggs were usually laid on the underside of leaves or along thin twigs or branches and hatched within 11.93 +/- 2.44 days (N=110).

Parasitoids

Of the 161 exposed eggs, only 8 (5.6%) successfully hatched into nymphs, while 66 were parasitized (40.4.%), 62 were presumed eaten (38.5%) and 25 failed to hatch (15.5%). This level of parasitism is consistent with parasitism rates in other systems (e.g. Mitchell and Mitchell1986). From all the parasitized eggs, only one species of parasitoid, *Gryon pentatomum* (Hymenoptera: Scelionidae: Scelioninae) was discovered (Fig. 4.. These parasitoids hatched approximately 13.02 +/- 3.52 days after hatching. Oviposition by *G. pentatomum* took approximately 10 minutes, after which the female would move on in search of another host (pers. obs). Once an egg was parasitized it was apparently not parasitized by any other wasps. Over the course of the present study, freshly emerged wasps were occasionally observed parasitizing unhatched eggs from the same clutch from which they had emerged. These ovipositions were successful and ultimately produced adult wasps.

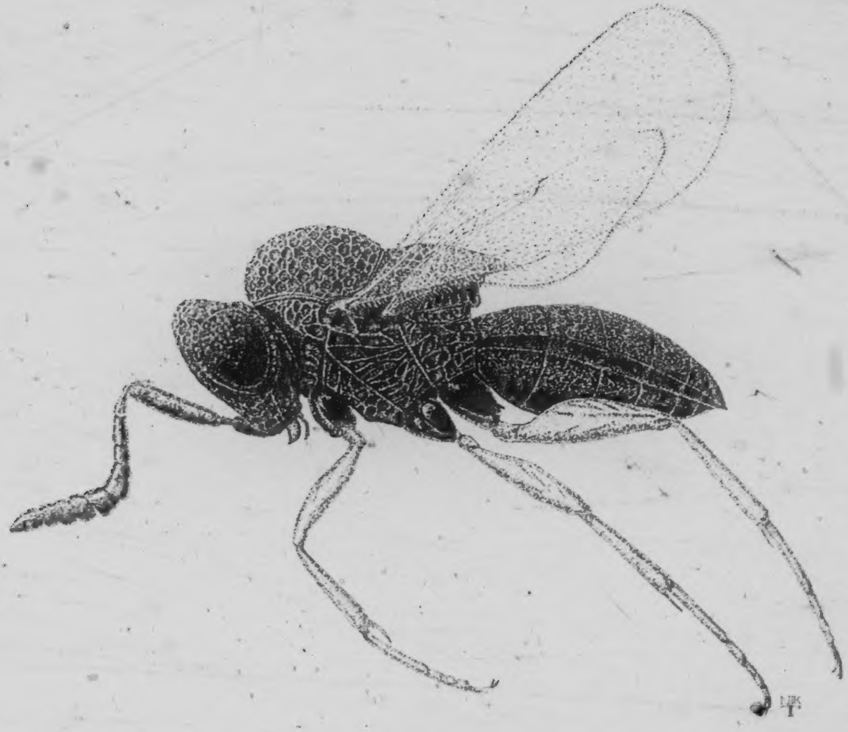

Figure 5.1. Lateral view of the scelionid wasp *Gryon pentatomum* (Dodd) 1913. (Female, length = 2 mm)

Predators

In addition to being targeted by parasitoids, Crusader bugs also experienced significant levels of predation. In this study, early instars were found to be highly susceptible to predation; this was especially true immediately after eclosion, when their cuticles had not yet hardened and they were most vulnerable. In one instance, 15 1st instars were predated by pharaoh ants, *Monomorium pharaonis* (Hymenoptera: Formicidae) over a span of only two hours while in captivity. Ants were ubiquitous throughout the pigeon pea crops, and probably played a significant role in controlling Crusader bug populations.

Crusader bug nymphs were also attacked by small, predatory big-headed bugs (Heteroptera: Lygaeidae: *Geocorinae*). Adults and nymphs of an unidentified species were occasionally seen attacking eggs as well as nymphs up to and including 3rd instar. Other predatory arthropods such as wasps, ground beetles and spiders were never seen feeding on adults, nymphs or eggs. In one instance, a predatory carabid beetle placed in a plastic container (200 mL) with a 3rd instar coreid died within 30 minutes, presumably due to exposure to the nymphs scent gland secretions, while the coreid remained unharmed.

Arthropods were not the only predators of Crusader bugs. Throughout the study, many birds were observed scouring the pigeon pea plants for insects. These included Common mynahs (*Acridotheres tristis*), Red-vented bulbuls (*Pycnonotus cafer*), Vaniroko broadbills (*Myiagra vanikorensis*) and Orange-breasted myzomelas (*Myzomela jugularis*). It is difficult to know exactly which predators consumed which eggs, however when entire clutches were completely missing (as was the case with all deliberately exposed eggs which were predated) this type of damage seemed most consistent with bird predation.

Discussion

Parasitoids

This is the first record of *Gryon pentatomum* from Fiji. Found in Australia and other Pacific Islands, this species is a generalist parasitoid, having been reared previously from *Mictis profana* on *Mimosa pigra* and *Acacia iteaphylla,* from *M. caja* on tomato and also from unidentified pentatomid eggs (Naumann and Steinbauer 2001). Parasitism and predation rates observed were consistent with other studies of parasitism by the genus *Gryon* in coreids (e.g. Mitchell and Mitchell 1986, Romeis *et al.* 2000).

Because female wasps were observed successfully ovipositing in eggs from the same clutch from which they had eclosed, *G. pentatomum* is capable of parasitizing eggs of various ages. This ability of the wasps to successfully attack eggs of various ages is highly desirable from a biological control standpoint, as it relaxes the need for the wasps to synchronize with their hosts' egg production in order to parasitize them. In a study of *G. pennsylvanicum* and other species, parasitoids were able to complete their development on hosts ranging from undifferentiated eggs to fully developed, uneclosed 1st instar nymphs (Nechols *et al.* 1989). This does not reflect female oviposition preference however, and in fact parasitization rates generally decreased with host age.

Host location by G. pentatomum

As shown in Chapter 4, *M. profana* males possess ventral abdominal glands, which appear to attract both males and females, ultimately leading to aggregations of these insects. This is similar to the findings of Yasuda (1990) who showed that males, females and nymphs of the coreid *Leptoglossus australis* were attracted to adult males. Using these male pheromones as a beacon, the scelionid parasitoid *Gryon pennsylvanicum* locates *L. australis* aggregations, thereby narrowing its search for host eggs (Yasuda and Tsurumachi 1994). It is highly likely that ventral abdominal glands in *M. profana* also have a kairomonal effect and are used by *G. pentatomum* for host location.

Predation

Despite assumptions that defensive glands would protect adults and nymphs from most predators, substantial predation of nymphs as well as eggs was observed. Ants in particular were especially capable of feeding on early instar nymphs and did so regularly. As generalist predators, ants are known to be significant mediators of pest species in many systems (Altieri 1994). Big-headed bugs, too, seemed undeterred by nymphal defensive compounds. Although many geocorines supplement their diets with plant material, they generally do not cause any significant plant damage and their importance as natural generalist predators of pests far outweighs the minor damage they may cause to crop plants (Frank and Slosser 1996).

Lastly, although birds were not directly observed feeding on *M. profana* or its eggs, they were seen gleaning the foliage for food, and quite possibly played a significant role in egg predation.

Conclusions

Many of the most effective pests are highly mobile (Rabb and Kennedy 1979). Hirose *et al.* (1996) suggest that this may be because predators and parasitoids might have difficulty in shifting their habitats to follow the seasonal movement of the pests as they move from one host plant to the next. *M. profana* is such a pest, capable of feeding on a wide variety of crops from several families. The ideal parasitoid in such situations is a generalist whose population can be maintained in the absence of the target host. Because *G. pentatomum* is a generalist parasitoid with multiple hosts and is able to oviposit in eggs of varying ages, it is an excellent biological control agent of *M. profana* and clearly has a large impact on Crusader bug populations. This beneficial impact might be compromised through pesticide use. Additionally, generalist predators are also excellent mediators of pest populations. In this system, ants, geocorine bugs, various species of birds are all generalists that probably contribute to controlling Crusader bug populations in Fiji.

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Chapter 6

Discussion and Conclusions

The Mictini *s.s.* are a tribe of coreid bugs from Asia, Australasia and Africa, characterized by unique and sometimes bizarre morphology. In combination, these characters suggest monophyly, yet at the same time the details seem to obscure the true relationships within the group. Many of the characters which make the mictines so easy to distinguish from one another are at the same time so wildly divergent that they are fairly useless for establishing common ancestry. At the same time, a given character may be very useful for establishing relationships in two distantly related groups of species. In the phylogenetic analysis presented in Chapter 2, a careful character-by-character analysis was used to help show what aspects of the phylogeny reconstructed in this thesis accurately depict the most probable history, and what relationships must remain ambiguous for the present.

The distribution of the Mictini *s.s.* throughout the Old World tropics is suggestive of a Gondwanan origin. This hypothesis was supported by my phylogenetic analysis, which suggests that the ancestors of some Asian Mictini had arrived in Asia by rafting on New Guinea, some 20 mya (Hall 1995, 1997). At the same time, other Asiatic taxa may have their origins in the West, either through colonization over land or by rafting on India, which collided with Asia about 15-20 mya (Turner *et al.* 2001). My phylogenetic analysis also provides a framework for useful revision of the genus *Mictis*. Through the removal and synonymy of several species, *Mictis* was restricted to 13 species. At the same time, the genus *Priolonomiopsis*, considered by previous workers (e.g. O'Shea 1975, O'Shea and Schaefer 1980) to be part of the now abandoned Derepteryx Group, has grown by two new species, *P. sumatra* and *P. sarawensis*, described herein.

Many of the characters used in this analysis are those that have historically been used in establishing mictine taxonomy. This includes many elaborate characters found only in males, upon which the majority of genus level distinctions have previously been founded. In Chapter 3, I showed that in *Mictis profana*, several of these characters- notably abdominal tubercles and hind limb armature- are highly sexually dimorphic and scale allometrically with respect to body length. Furthermore, examination of numerous museum specimens of several species revealed that because of these strong allometric relationships, many of these 'diagnostic' characters may be greatly reduced or even absent in small individuals. From a taxonomic standpoint this reminds us of the potential risks of using highly variable characters for establishing taxonomic relationships.

The selective pressures driving the scaling relationships of these dimorphic characters were then explored in Chapter 4, where I showed that mating in *Mictis profana* is non-random and probably involves sexual selection acting on both courtship and agonistic behaviour. My observations provide the first published descriptions of mating behaviour in a species of *Mictis*. I established that males attempted to mate with multiple females, some willing and others not, and fought one another for territory and for the mates that would come there to feed. Large males with strong femora and large abdominal tubercles were able to secure territories and mated more often. With competition for mates high, males guarded females for hours on end, fighting off would-be suitors as they came to court. In this respect, the mating system of *M. profana* includes a strong element of resource defence polygamy.

From their perspective, females were ultimately the judges of who would be allowed to mate, as they could never be forced into mating and were usually the ones who would terminate copulation. Many females did not resist prolonged mating as long as food was available. Perhaps they acquiesced to suitors not only to receive their sperm but also for the protection they would provide from other males, thereby allowing them to feed in peace.

In the final data Chapter I studied *M. profana* as a pest of pigeon pea and eggplant in Fiji, and explored the potential to limit damages with biological control. *M. profana* is a highly mobile pest capable of feeding on several crops, making it potentially difficult for predators and parasitoids to track them (Hirose *et al.* 1996). Like other coreids it is also protected by potent defensive secretions, and is not expected to suffer significant predation or parasitism (Steinbauer 1999, Steinbauer & Davies 1995.). During the course of this study however, surprisingly high rates of predation on nymphs and eggs were observed, with ants and big-headed bugs apparently unaffected by the defensive compounds. Additionally, a new species record was established for Fiji with the rearing of the parasitoid *Gryon pentatomum* from eggs laid on pigeon pea.

It is surprising that such a unique and physically striking group as the Mictini has remained relatively unstudied for so long. The taxonomy of this group has received almost no attention since O'Shea and Schaefer's contributions in the late 1970's and early 1980's. This is possibly because of the daunting amount of revisionary work that still needs to be done, with hundreds of species distributed throughout Africa and Asia, plus innumerable unknown species yet to be identified and placed taxonomically. This thesis has clarified the concept of *Mictis* as a genus and laid a basis to accommodate further work on the Mictini. Perhaps recent advances in molecular techniques may soon be applied to help unravel the complex and old relationships between the Asian and African faunas, which may in turn shed light on the biogeographic history of these bugs.

This thesis also illustrates that the Mictini provide an excellent model to study various aspects of evolution and ecology. For example, the extreme variability in sexual dimorphic structures, particularly with respect to abdominal tubercles, provides an excellent framework for comparative studies of sexual selection and functional morphology.

With distributions spanning the Old-World tropics, the Mictini are not easily accessible to many researchers. This is exacerbated by the fact that many tropical nations are either politically unstable, or else have neither the infrastructure nor the funding to accommodate domestic or foreign researchers. Furthermore, in the face of rapid habitat loss and degradation, the days of many mictine species are probably numbered. Rather than being dismayed by these factors, I instead choose to be hopeful that other researchers may see the potential that this group of insects possesses, in terms of their taxonomy, systematics, biogeography, and life history. It is my hope that the results of this thesis might provide the stimulation and the foundation for future work on this group.

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Appendix 1. Data matrix of 67 morphological characters for 29 taxa. Missing data are coded as "?"

	Characters																	
										1								
Taxon Name	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8
Mictis amboinensis	0	0	0	2	0	1	0	0	1	0	1	0	1	2	0	1	0	0
Mictis caja	0	0	0	1	0	1	0	0	1	0	1	0	1	2	0	1	0	1
Mictis discolor	0	0	0	1	0	1	1	0	1	0	1	0	1	0	2	0	0	0
Mictis longicornis	1	1	0	1	1	1	1	0	1	0	1	0	1	0	2	1	0	1
Mictis profana	0	0	0	2	0	1	0	0	1	0	1	0	1	2	0	1	0	0
Mictis pungens	0	1	0	1	1	1	1	0	1	0	1	0	1	0	2	?	0	0
Mictis tenebrosa	0	1	0	1	0	1	0	0	1	0	1	0	1	0	1	0	0	0
Mictis farinulenta	0	0	0	1	1	1	1	0	1	0	1	0	1	1	0	1	0	0
Mictis gallina	1	1	0	1	1	1	1	0	1	0	1	0	1	0	2	0	0	1
Mictis serina	0	0	0	1	0	0	0	0	1	0	1	0	1	2	2	1	0	1
Mictis formidabilis	?	?	0	1	?	?	?	0	1	0	1	0	?	?	1	1	0	0
Mictis oceanensis	?	?	0	1	?	?	?	0	1	0	1	0	?	?	0	1	0	0
Aspilosterna acutangula	0	0	0	1	1	1	1	0	1	0	1	0	0	0	2	0	0	0
Mercennus gracilis	0	0	1	3	0	1	0	0	1	0	1	0	1	1	1	0	0	1
Neomictis filicornis	1	1	0	1	0	0	0	0	1	0	0	1	1	1	2	1	0	1
new sp. from Sumatra	0	0	0	1	0	1	0	0	0	0	1	1	1	1	1	0	0	1
new sp. from Sarawak	0	1	0	1	0	0	0	0	0	0	1	0	?	?	?	?	0	1
Notobitopsis aruana	0	1	1	3	0	1	0	1	1	0	0	1	1	1	1	0	0	1
Notobitopsis militaris	0	1	1	3	0	1	0	1	1	0	0	1	1	1	1	?	0	1
Priolonomiopsis amplicollis	0	1	0	1	1	0	0	0	0	0	0	0	1	0	?	0	0	1
Pseudomictis distinctus	0	1	0	1	0	1	0	0	1	0	0	0	1	1	1	1	0	1
Pseudomictis obtusispinus	0	1	0	1	0	1	0	0	1	0	0	0	1	1	1	0	0	1
Pternistria sexlineata	0	0	0	1	0	0	1	0	1	1	1	1	1	1	1	0	0	1
Xyrophoreus tonsor	0	0	0	1	1	1	1	0	1	0	1	0	1	1	0	1	0	1
Molipteryx hardwickii	0	0	0	1	0	0	0	0	0	0	2	1	0	0	1	0	0	1
Priolonomia gigas	0	0	0	1	0	0	1	0	1	0	1	1	0	0	1	1	1	1
Ochrochira pallescens	0	0	0	1	0	0	?	0	0	1	1	0	1	0	1	1	0	1
Elasmopoda sp.	0	0	1	0	0	1	0	0	1	0	1	1	1	1	0	?	0	1
Plectropoda bicolor	0	0	0	1	0	1	0	0	1	0	1	0	1	0	0	0	0	1

Appendix 1. Continued.

	Characters																	
		2									3							
Taxon Name	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6
Mictis amboinensis	1	0	1	1	1	1	3	0	0	0	1	0	0	0	1	1	1	1
Mictis caja	1	0	1	1	1	1	3	0	0	0	1	0	0	0	1	1	1	1
Mictis discolor	1	0	0	1	0	1	3	0	0	0	0	0	0	0	1	1	1	0
Mictis longicornis	1	0	0	1	0	1	3	0	0	0	1	1	0	0	1	1	1	1
Mictis profana	1	1	1	1	1	1	3	0	0	0	1	0	0	0	0	1	1	1
Mictis pungens	0	0	1	1	0	2	1	0	0	0	1	1	0	0	1	1	1	1
Mictis tenebrosa	1	0	0	1	1	1	3	0	0	0	1	1	0	0	1	1	1	1
Mictis farinulenta	0	1	1	1	1	2	3	1	1	0	1	0	0	0	1	?	1	0
Mictis gallina	1	0	0	1	0	1	3	0	0	0	1	1	0	0	1	1	1	1
Mictis serina	1	0	0	1	1	1	3	0	0	0	0	0	0	0	1	0	1	1
Mictis formidabilis	0	0	1	1	0	2	1	0	0	0	1	1	0	0	1	0	1	1
Mictis oceanensis	1	0	1	1	1	1	3	0	0	0	1	0	0	0	1	?	1	1
Aspilosterna acutangula	0	2	0	1	0	1	3	0	0	0	1	0	0	0	1	0	1	0
Mercennus gracilis	1	0	0	0	0	0	0	0	0	1	0	0	0	0	1	?	0	0
Neomictis filicornis	1	0	1	1	0	1	2	0	0	0	1	0	0	0	1	0	1	1
new sp. from Sumatra	1	1	0	1	1	2	3	0	1	0	1	0	0	0	1	?	1	1
new sp. from Sarawak	1	1	0	1	0	2	1	0	1	0	1	0	0	0	1	?	1	0
Notobitopsis aruana	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Notobitopsis militaris	1	0	1	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Priolonomiopsis amplicollis	0	1	0	1	0	2	3	0	1	0	2	0	0	0	1	?	1	1
Pseudomictis distinctus	0	2	0	1	0	0	3	0	0	1	0	0	0	0	1	?	0	1
Pseudomictis obtusispinus	0	1	0	1	0	0	3	0	0	1	0	0	0	0	1	0	0	1
Pternistria sexlineata	1	1	1	0	1	1	3	0	0	0	1	0	0	0	1	0	0	1
Xyrophoreus tonsor	1	0	0	1	0	1	3	0	0	0	0	0	0	0	1	0	1	1
Molipteryx hardwickii	1	0	1	1	0	2	3	1	1	0	2	0	0	1	0	1	0	0
Priolonomia gigas	0	0	1	1	0	2	3	1	1	0	2	0	1	0	1	1	0	0
Ochrochira pallescens	1	0	1	1	0	2	3	0	1	0	1	0	1	0	0	1	0	0
Elasmopoda sp.	0	0	0	1	0	1	3	0	0	0	0	0	0	0	1	1	1	1
Plectropoda bicolor	1	1	0	1	0	1	3	0	0	0	0	0	0	0	0	1	1	1

Appendix 1. Continued.

	Characters																	
				4										5				
Taxon Name	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	3	4
Mictis amboinensis	1	1	0	0	0	0	0	2	0	0	1	0	1	1	0	0	1	0
Mictis caja	1	1	0	0	0	0	0	2	0	0	1	0	0	1	0	0	1	0
Mictis discolor	1	0	0	0	0	0	1	3	0	0	0	0	1	1	2	0	0	0
Mictis longicornis	1	2	0	0	0	0	0	3	0	1	0	0	0	1	2	0	0	0
Mictis profana	1	1	0	0	0	0	0	2	0	0	1	0	1	1	0	0	1	0
Mictis pungens	1	2	0	0	0	0	0	3	0	1	1	0	0	1	0	0	0	0
Mictis tenebrosa	1	1	0	0	0	0	0	2	0	1	1	0	1	1	0	0	0	0
Mictis farinulenta	?	0	0	0	0	0	0	2	0	0	1	0	1	1	0	0	0	0
Mictis gallina	1	2	0	0	0	0	0	3	0	1	0	0	0	1	2	0	1	0
Mictis serina	0	1	0	0	0	0	0	3	0	0	0	0	0	1	0	0	0	0
Mictis formidabilis	1	2	0	0	0	0	0	2	1	?	1	0	1	0	0	0	0	0
Mictis oceanensis	1	1	0	0	0	0	0	2	0	0	1	0	1	1	0	0	0	0
Aspilosterna acutangula	0	1	0	0	0	0	0	3	0	0	1	0	0	1	0	0	0	1
Mercennus gracilis	2	0	1	0	0	1	0	2	2	0	2	0	0	0	2	0	2	0
Neomictis filicornis	1	2	0	0	0	0	1	3	0	1	1	0	1	1	2	0	0	0
new sp. from Sumatra	1	1	0	0	0	0	0	1	1	0	3	0	0	0	0	0	0	0
new sp. from Sarawak	1	1	0	0	0	0	0	3	0	0	2	0	0	0	0	0	0	0
Notobitopsis aruana	2	0	0	0	0	0	0	3	0	0	1	1	0	1	2	0	0	0
Notobitopsis militaris	2	0	0	0	0	0	0	3	0	0	1	1	0	1	2	0	0	0
Priolonomiopsis amplicollis	0	1	0	0	0	0	0	1	1	0	3	0	1	0	0	0	1	0
Pseudomictis distinctus	2	0	0	0	1	0	1	3	2	0	2	1	0	0	2	0	0	0
Pseudomictis obtusispinus	2	0	0	0	0	0	0	3	2	0	2	1	0	1	2	0	0	0
Pternistria sexlineata	2	0	1	0	1	0	0	3	2	0	2	1	0	0	1	0	2	0
Xyrophoreus tonsor	1	2	0	0	0	0	1	3	0	0	0	0	0	1	0	0	0	0
Molipteryx hardwickii	2	0	1	1	0	0	0	3	0	0	1	0	1	1	0	0	0	1
Priolonomia gigas	0	0	1	1	0	0	0	2	1	0	1	0	1	0	0	0	1	1
Ochrochira pallescens	2	0	1	1	0	0	0	1	0	0	1	0	1	1	0	0	0	1
Elasmopoda sp.	1	1	0	0	1	0	0	3	2	0	2	1	0	0	1	1	0	0
Plectropoda bicolor	1	1	0	0	1	0	0	3	2	0	2	0	0	0	2	1	1	0

Appendix 1. Continued.

	Characters									
						6				
Taxon Name	5	6	7	8	9	0	1	2	3	4
Mictis amboinensis	1	0	1	1	1	2	2	1	1	0
Mictis caja	0	3	1	1	1	2	2	1	1	0
Mictis discolor	0	0	0	1	1	0	1	0	0	0
Mictis longicornis	0	0	0	1	1	2	1	1	0	0
Mictis profana	1	0	1	1	1	2	2	1	1	0
Mictis pungens	0	0	?	1	1	2	1	1	0	0
Mictis tenebrosa	0	1	1	1	1	2	2	1	1	0
Mictis farinulenta	0	0	1	1	1	2	2	1	0	0
Mictis gallina	0	1	0	1	1	1	1	0	0	0
Mictis serina	0	0	0	1	1	2	2	1	0	0
Mictis formidabilis	0	?	1	0	0	2	1	1	?	0
Mictis oceanensis	0	?	?	1	1	2	2	1	1	0
Aspilosterna acutangula	0	0	0	1	1	2	2	0	0	0
Mercennus gracilis	0	0	?	0	0	2	3	1	1	1
Neomictis filicornis	0	2	0	1	2	2	1	1	0	0
new sp. from Sumatra	0	0	?	0	0	2	1	1	0	0
new sp. from Sarawak	0	0	?	1	1	2	1	1	1	0
Notobitopsis aruana	0	0	1	1	1	1	1	1	1	0
Notobitopsis militaris	1	0	1	1	1	1	1	1	1	0
Priolonomiopsis amplicollis	0	0	?	0	0	2	1	1	0	0
Pseudomictis distinctus	0	0	3	1	1	2	3	2	1	0
Pseudomictis obtusispinus	0	0	3	1	1	2	1	2	1	0
Pternistria sexlineata	0	0	?	2	1	2	3	0	1	0
Xyrophoreus tonsor	0	2	0	1	1	2	1	0	0	1
Molipteryx hardwickii	0	0	0	0	0	0	0	0	0	0
Priolonomia gigas	0	0	2	0	0	0	0	0	0	0
Ochrochira pallescens	0	0	0	1	1	0	0	0	0	0
Elasmopoda sp.	0	2	?	2	1	2	3	0	0	0
Plectropoda bicolor	1	0	3	2	1	2	3	2	0	0